ECOLOGY

Vol. 41 OCTOBER, 1960 No. 4

TIME AND SPACE AND THE VARIATION OF SPECIES

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Introduction

It is not intuitively obvious why a square yard of meadow, say, should not be exactly like the next square yard in species-composition, yet it must have been noted many times, and from the earliest times, that it rarely or never is so. Yet a few square yards may contain a large fraction of all the species of plants that can be found on an acre. This approximate sameness, yet unequivocal and persistent difference, reached "the literature" at least a hundred years ago (Williams 1943b), and became an active subject of discussion in the present century.

If we observe moths as they enter a light trap, we may very likely find that the first half dozen are all of different species. The same thing may happen if we note the singing males on an early morning bird count in May; and it may happen again if we note the species of trees in a tropical forest. At first we have as many species as individuals, but in all cases the ratio of species to individuals falls rapidly as our observations increase, and we soon reach the point of diminishing returns. However, we never seem to reach the point of zero returns, though ultimately the ratio of individuals to species may run into the hundreds of thousands.

When we are dealing with botanical material, the subject centers around the concept of the species-area curve, where the early work goes back to Arrhenius (1921) and Gleason (1922). Here we are dealing with a phenomenon that concerns the space under observation. Williams (1943) made the comment that "Doubling the time of trapping (of moths in a light trap), at any level, except for very small samples, always adds about thirty species to the total." This is a restatement of Gleason's expectations, but refers to time instead of space. Preston (1948) commented that the rule would necessarily hold, to a first approximation, over a fairly long range of observations, if we were taking increasingly large samples from a fixed lognormal distribution. But since, in practice, the universe being sampled tends to increase as the sample itself increases, complications can occur. None the less, Williams' observation does raise the question as to how far time and space may be essentially equivalent in some ecological problems.

In a companion paper I hope to show that if we have a series of independent, isolated, populations or "universes," then the relation between species and individuals should, on theoretical grounds, follow not the Gleason law but the Arrhenius one to a very close approximation. This laws states that

$$N = kA^z$$

where N is the number of species on an area A, and k and z are constants which Gleason treated as arbitrary and to be found by observation. In the other paper it will be shown that, for the conditions above specified, z should be 0.27 approximately, and k can be defined in terms of the density of individuals to the unit area. Thus there are no strictly arbitrary constants.

Most often in dealing with species-area curves we are dealing with a geographical continuum, in which small areas are portions of the larger ones. Under these circumstances, the small areas tend to act as "samples" of larger ones, though we cannot define the size of the larger ones of which a given collection is a sample, except by the internal evidence of the sample itself (Preston 1948). It is a property of such samples that the ratio of species to individuals is much higher than in the complete "universe," and the distribution is a truncated lognormal, not a complete one. When we translate this from species/individuals to species/area, this means that small areas tend to be over-rich in species. They receive an enrichment from contiguous areas, which they could not do if they were complete isolates.

The relation between the size of an area and the number of species it holds has been largely the province of plant ecologists. Thus Vestal (1949) gives tabulations of species-area relationships for about 300 instances of plants but only 3 for animal groups. From the time of Clements onwards and perhaps before, there has been a belief that a stand of vegetation, comprising a number of species, constitutes a "community" (Oosting 1948), though Gleason's (1936) views quoted by Watts (1947) seem contrary: "The final step is Gleason's: to him the plant association is merely a fortuitous juxtaposition of plant individuals." Underlying the concept that the community may be a genuine organic unity, however, is frequently a second concept, that the rarer species are not essential to it. This is similar to the views of petrographers who consider that to qualify as a true granite a rock must contain quartz, felspar, and mica, the "essential minerals," while minor ingredients such as sphene and zircon are merely "accessory" minerals. On this view the plant association can be defined by its more plentiful species, the rest being regarded as merely adventitious, and a great deal of the literature is therefore concerned with the problem of what minimal area is sufficient (Cain 1938, Hopkins 1957). From this point of view a minimal area is one that will make sure that the "essential" ingredients are present. From the point of view of the present paper the idea is a faulty one: a sufficient area or quadrat is one which will give the same count, rarities included, as another quadrat of the same size. In practice this does not happen at any size of quadrat, so that no size of quadrat is absolutely satisfactory.

In the present paper we propose to proceed empirically, as was done by earlier writers, and to find out what actually is the appearance of the species-area curve, for one or 2 specific instances, over its complete range. We shall do this for the breeding birds of an area, and the area will extend from an acre or so to continental and global areas. Then, having studied species-area or species-space as being more accessible to us, in a big way, than a species-time curve, because we do not know in much detail what happens over vast stretches of time, we can speculate that time and space may be equivalent variables, and see if the known facts fit that hypothesis.

Succession

The resemblance between time and space, in its simplest form, may be seen by driving a stake into the open water of a lake and then taking a transect toward the shore. We pass first through planktonic vegetation, then perhaps water lilies, then marsh, then grassland, then a succession of forest stages to climax forest. But we can pass through the same succession in the same order without moving at all. We may just sit by the stake for a few years or centuries and the seral stages will come to us one after the other as the lake fills in or drains.

Since there is so much literature on species-area properties, and on succession, I hope I may be forgiven for not reviewing it all except where it seems especially pertinent to the equivalence of time and space. In the present paper we are concerned with changes brought about by the lapse of time, whether they are regarded as mere fluctuations without any particular direction, or as methodical "succession" as that is usually understood, or as evolution when the time scale is long. Similarly, we are concerned with changes in the ecological set-up as we go from place to place, whatever the cause or causes of that change. The more obvious causes might be variations in the underlying geological formations or the character of the soil, variation in altitude or aspect, and, on a large scale, in climate, rainfall, temperature, or the different geological histories of the various regions of the earth.

As we go to longer and longer times, from a few thousand years to a few million, "succession" passes by degrees into "evolution" as ordinarily understood or is superseded by evolution, and it would be still less possible to review the literature of that subject. It seems sufficient here to concede that there will be changes of species with time and not to attach particular labels to those changes.

THE SPECIES-AREA CURVE

The precise form that the species-area curve takes will vary according to the place where we begin. We shall get somewhat different curves if we place our first quadrat in the eastern North American deciduous forest or in the lowland neotropical forests of Panama. Having chosen a place to begin, we should double our area by taking in a contiguous or adjacent similar area, or as similar and as nearby as we can. This is the same principle as applies in *time.* If we count moths this year, we should double the collection by trapping next year, and not wait 50 years and then trap for a second year.

Since there is more information about the birds of the eastern deciduous forest, we should first examine them. In the nearctic it is sometimes estimated that there is about one pair of birds per acre, averaged over the whole region. In the deciduous forest it tends to run higher, perhaps 2 or 3 pairs per acre (see below, on the birds of "Neotoma"). But in this forest there can be found breeding 200 or 300 species, so that if all species were equally common and a 2nd pair of species could not be fitted in until every other species was represented by one pair, the minimum area that would achieve representation of all species would be around 100 acres. But some birds are vastly more common than others, thousands of times commoner, and their distribution is not regularized but more nearly random. It follows that even 100,000 acres will rarely achieve full representation of species, and that another 100,000 acres will not be identical in its count. None the less, much smaller areas give interesting information. In particular, it will be found that areas of equal size tend to give roughly equal numbers of species, if we avoid choosing areas that are, for instance, half forest and half marsh. Thus it becomes possible to construct a species-area curve which does not have excessive "scatter" or dispersion of the observed points from a single curved line.

Methods of plotting

In much of the work on plant associations and the species-area curves of such associations, the quadrats are increased in size or in number in a geometric progression, but none the less the results are plotted by some writers on an arithmetical scale for both area (as abscissa) and number of species (as ordinate). This seems illogical. It results in the observed points being crowded toward the left hand end, or origin, of the curve, and in their being very sparse toward the right hand end. If the areas are increased in geometric series, the plotting should normally be on a logarithmic base, thus making the spacing of the points uniform.

If however the double-arithmetical plotting is used, it becomes apparent that the curve approximates in many cases to a generalized parabola, with its vertex at the origin and axis horizontal. See, for example, Hopkins (1957). Such a curve would become a straight line on a "log-log" plot, *i.e.* if both ordinate and abscissa are plotted logarithmically. This is, in effect, what Arrhenius (1921) did, though he provided no graphs, only the data for them.

While logic, in the first instance, and experience of the results in the second, seem to call for a logarithmic scale for abscissae, it is only experience that can decide whether the ordinate should be so plotted. Gleason (1922) seemed to get better results with arithmetical ordinates. In the present paper we use both methods for the same data, the "Gleason plot" for Fig. 1, the "Arrhenius plot" for Fig. 2. Each has its uses, and neither produces a straight line over the whole range of the graphs; and there are sound reasons for not expecting it to.

Statistical Difficulties of Some Earlier Plots

For the purposes of some of the earlier writers, particularly when they were concerned with the defining of communities in terms of a few of the commonest species, the quadrats had to be small or they got too many species. This is exactly the opposite of the situations generally desired in the present paper. Here the fundamental problem is not how small the quadrat can be made and yet define a community, but how many species we must have in order to obtain statistical utility. In general we should like this to be 100 species or more, though we must sometimes settle for half that number. But in the early quadrat studies the number of species was often less than 10, sometimes only 2 or 3, and rarely much more than 20. Whatever results flow from studies of this, the extreme left end of the complete curve, they are not necessarily, or apparently usually, applicable to studies of the main part of the curve, as will be seen from Fig. 2. This difference between the initial and central parts of the species-area curve may influence our attempts to reconcile the present findings with those of MacArthur (1959) or Kohn (1958) and others, which deal chiefly with small numbers of species (see Hairston 1959).

Log-Log Plottings

The Arrhenius Equation

We may derive this empirically as follows. We can expect that in almost all cases increasing the area will tend to increase the total number of species. It cannot decrease it. We can imagine a situation, which some quadrat specialists would consider ideal, where the 2nd and subsequent quadrats were identical with the first. Then if S is the number of species and A the area (in acres or any other unit)

$$S = KA^0, \text{ where K is a constant} \qquad (1)$$

since A^0 is unity.

That however is not the kind of world we live in.

We can next imagine a situation where nothing on the 2nd quadrat resembles anything on the first. Perhaps there are exactly as many individuals and exactly as many species, but there are *no* species common to the 2 quadrats. Such a situation approximately exists if we take as our quadrats Australia and the continental United States, which are of equal size but well isolated from each other for geological lengths of time. In that case we should have

$$S = KA \qquad (2)$$

where A is to the first, not the zeroth, power.

Strictly speaking this in not a *limiting* case, if we can choose to take our areas or quadrats in the order a — b, and refuse b — a, for the 2nd area might be much richer in species than the first. This would be the case if we added South America to the nearctic for instance. But by stipulating that we must strike an average of the a — b, and b — a arrangements, equation (2) becomes essentially a limit.

It will now be obvious that the simplest assumption we can make is that in real life

$$S = KA^z \qquad (3)$$

where z is an exponent somewhere between zero and unity.

We have derived this equation in an empirical fashion, partly because it does, under some circumstances, approximate the theoretical relationship for complete lognormal ensembles, and partly because our Fig. 2 is an "Arrhenius" plotting, in the sense that a log-log plotting should give a straight line if the Arrhenius equation is observed. Since, however, our purpose is not to check the Arrhenius equation but to ascertain the degree of resemblance between time and space, we are not here justified in pursuing the matter further.

Ideal Method of Obtaining Increasingly Large Areas

What we should like to do is to take as a "core" an area in the form of a circle with a radius of a quarter of a mile. It would have an area of about 125 acres. Then from the same center we would describe circles of greater radius, in the ratio of $\sqrt{2}$, 2, 2 $\sqrt{2}$, 4, 4$\sqrt{2}$, and so on, thus doubling the area every time and expanding equally in all directions. The areas would become 250, 500, 1000, 2000, etc., and the radii would include, at every second step, ½ mile, 1 mile, 2 miles, etc.

If we could do this, starting from a dozen or twenty "cores" in the deciduous forest area[2], we could get an average picture that would be very useful. But we have no such information and must depend on less ideal selections.

The Nearctic Avifauna, beginning in Western Pennsylvania

In Table I are listed some dozens of counts and estimates of the number of species of birds breeding on areas of different sizes in the nearctic. It was not possible to begin at a single point and extend the count by doubling and redoubling by the use of strictly contiguous areas. We did the best we could in that respect, beginning with small areas in western Pennsylvania, but taking other samples in Ohio and other nearby states. These areas are treated as independent samples and are not combined. They merely serve to confirm that areas of a particular size in this general area tend to have about the *same number* of species though they may not be the *same* species. We then consider the counts of counties and similar areas, and by degrees we progress to the whole of western Pennsylvania as defined by Todd (1940) and to other statewide estimates of breeding species. Where two counties are contiguous we have sometimes combined their areas and their counts, thus getting an additional point on our curve; and we have used the same tactics with the states, first combining western Pennsylvania and West Virginia, then combining these with Ohio, then adding in turn New York State, Maryland, Indiana, and Illinois. In each case the addition has a substantial boundary in common with the preceding area, so that we are dealing with a geographical continuum. We next take the eastern United States up to the 100th meridian (but not the eastern part of Canada) and then the nearctic exclusive of Greenland. Our next step takes in the whole world.

I am indebted to many collaborators for the estimates recorded in Table I: most of it is unpublished information and has been obtained by correspondence. Their names are given in Table

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[2] The term "Eastern Deciduous Forest" as used in this paper frequently means the region in which the deciduous forest is the typical natural cover, and does not specifically mean the woodland facies of this region. It will be obvious, I think, from the context just what is meant. Even under natural conditions the region includes, in the west, areas of prairie, and in the east, areas of salt marshes and seashores. Several states have frontages on Lakes Erie and Ontario, and most have smaller lakes, large rivers, and fresh-water marshes; along the high ridges of the Alleghenies are "balds" and spruce forests, and under the disturbed conditions of the present day are unnatural grasslands and cultivated areas. Except for quite small areas, it is impractical to segregate out the woodland areas from the rest, still less to make distinction of the several sorts and seres of forest, very little of which is climax of any sort. The text will usually make clear with what we are dealing when we speak of the "forest." "Eastern" refers to eastern North America.

TABLE I. Species-area information, beginning in the eastern North American deciduous forest country. Reference numbers B begin in neotropical

Ref. No.	Area (acres)	Locality	Species breeding in one year	Authority
1	0.5	Butler, Pa.	4	Preston
2	6	Butler County, Pa.	18	Earl Schriver
3	23	Eastern U.S.A.[1]	23	Audubon Breeding Bird Counts
4	62	Eastern U.S.A.[2]	32	Audubon Breeding Bird Counts
5	69	Hocking Co., Ohio[3]	43	Ed S. Thomas
6	90	Butler County, Pa.[4]	42	Norris (1947)
7	130	Temple Hollow, Beaver County, Pa.	38+	R. Edeburn
7a	150	"Sapsucker Woods", Ithaca, New York	65	A. A. Allen
8	482	Near Chicago, Illinois	72	Beecher (1942)
9	1.7×10^{4}	Western New York State	87	Saunders (1936)
10	2.04×10^{5}	Caroline County, Indiana[5]	79	Chandler Robbins
11	2.19×10^{5}	Lucas County, Ohio	105	Louis W. Campbell
12	2.36×10^{5}	Monogalia Co., W. Va.	107	Maurice Brooks
13	2.85×10^{5}	Beaver County, Pa.	88	W. E. Clyde Todd
14	2.87×10^{5}	Pymatuning, Pa.	113	Grimm (1952)
15	2.1×10^{5}	Prince Georges Co., Maryland	105	Chandler Robbins
16	3.9×10^{5}	Jackson County, Illinois	88	Richard Brewer & Chas. Kendeigh
17	4.19×10^{5}	Preston Co., W. Va.	125	Maurice Brooks
18	4.55×10^{5}	State College, Pa.[5]	80	Merrill Wood
19	6.33×10^{5}	Cayuga County, New York[6]	122	Allen H. Benton
20	6.5×10^{5}	Champaign County, Illinois	82	Richard Brewer & Chas. Kendeigh
21	6.55×10^{5}	Monongalia & Preston Cos., West Va.	123	Maurice Brooks
22	6.6×10^{6}	Maryland (State)	177	Robert E. Stewart & Chandler Robbins
23	1.54×10^{7}	West Virginia (State)	162	Maurice Brooks
24	1.57×10^{7}	Western Pennsylvania	168	W. E. Clyde Todd
25	2.3×10^{7}	Indiana State[7]	141	Val Nolan, Jr.
26	2.65×10^{7}	Ohio State	177	Ed S. Thomas
27	3.11×10^{7}	W. Pa. and W. Va.	180	W. E. Clyde Todd & Maurice Brooks
28	3.19×10^{7}	New York State	191	E. M. Reilley & Kenneth C. Parkes
29	3.47×10^{7}	Illinois State	156	Melvin Traylor
30	5.76×10^{7}	W. Pa., W. Va., Onio	191	
31	8.94×10^{7}	W. Pa., W. Va., Ohio, N. Y.	222	
32	9.6×10^{7}	W. Pa., W. Va., Ohio, N. Y.	234	
33	1.19×10^{8}	All above plus Indiana	237	
34	1.54×10^{8}	Add Illinois	240	
35	9.3×10^{8}	Eastern U.S.A.	317	Peterson (1947)
36	4.6×10^{9}	Nearctic, excluding Greenland	625	Kenneth Parkes
37	1.25×10^{11}	Whole Earth	8600	
B 1	3.75	San Isidro del General, Costa Rica	c30	Alexander Skutch
B 2	15	Vera Cruz State, Mexico	84	Davis (1952)
B 3	15	Vera Cruz State, Mexico	102	Davis and Morony (1953)
B 4	15	Vera Cruz State, Mexico	106	Davis (1955)
B 5	600	Barro Colorado Island	c150	Eisenmann (1952)
B 6	6×10^{5}	Panama Canal Zone and adjoining	c343	Sturgis (1928)

(TABLE I. Continued)

Ref. No.	Area (acres)	Locality	Species breeding in one year	Authority
B 7	1.8×10^{7}	Republic of Panama	680	Eisenmann (1955)
B 8	6.4×10^{8}	Middle America (Panama to Mexico, inclusive)	1181	Eisenmann (1955)
B 9	5.13×10^{9}	Middle America plus Nearctic	1503	

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[1] 1951, Average of 26. Audubon Field Notes Vol. 5. pp. 316 *et seqq.*

[2] 1951, Average of 4.

[3] Average of 10 years at Neotoma.

[4] Average of 2 years. Preston Laboratory grounds.

[5] A minimum.

[6] 1949—Breeding Birds of Cayuga Co. (Unpublished).

[7] Regular breeders only: estimate may be conservative.

I, and where no date follows the name, it should be assumed that it is information by correspondence in the years 1956-1958. We attempted to obtain uniformity of treatment by specifying, in the case of counties and larger areas, that only *regular* breeders would appear on the lists used for Table I, and "regular" breeders were defined as those that certainly nested within the area in 9 years out of 10. For most species this presents

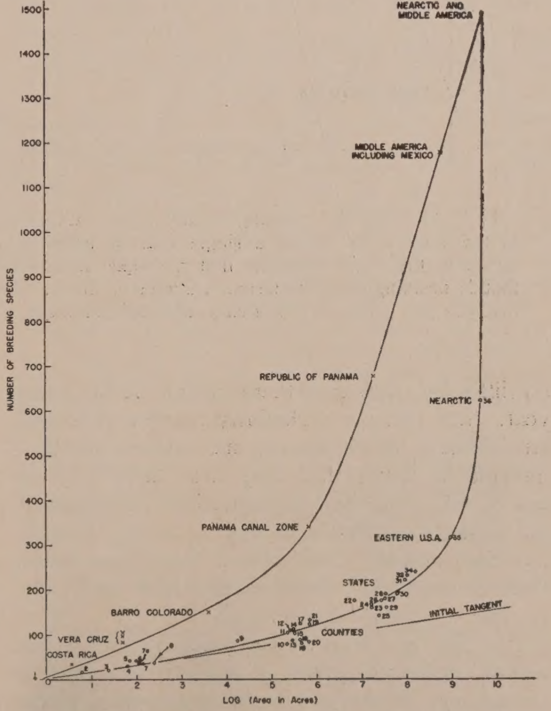

FIG. 1. Birds of the nearctic and neotropical Regions. Number of breeding species for various sizes of area = abscissa logarithm. The lower, or nearctic, curve starts in the deciduous forest of eastern North America. The Costa Rica point on the upper curve is believed by Dr. Skutch to be higher than typical. (This is a "Gleason plot").

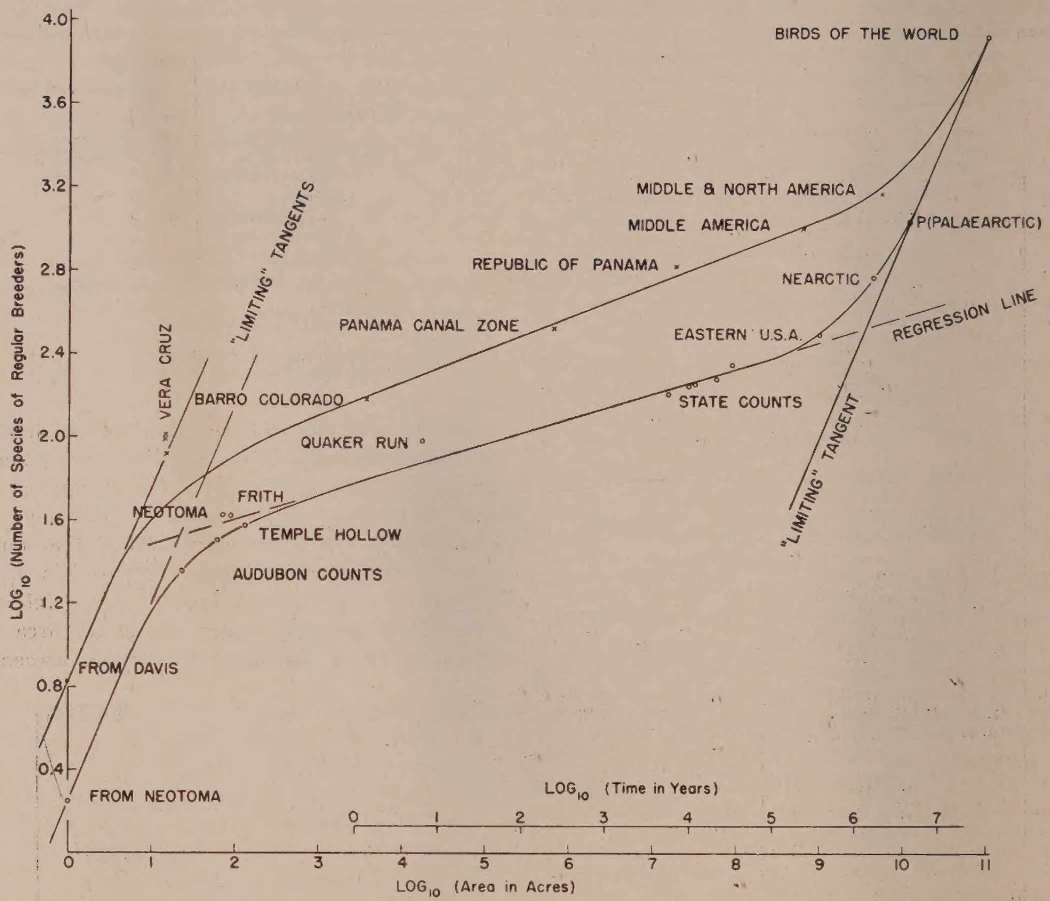

FIG. 2. "Log-log" plotting of the same data as in Fig. 1. A time-scale has been added as an alternative to the space-scale. Since a single year or breeding season (log time = 0) is the shortest time with any meaning, the graph suggests that a couple of thousand acres in the smallest area of eastern deciduous forest that is meaningful in species-area studies of birds. This assumes that space and time are "equivalent," and that the two scales are correctly adjusted sideways. This is an "Arrhenius plot."

no difficulty; they nest there unequivocably every year. But there is a shadowy margin of irregular breeders which usually nest there, but it is difficult to assert that they nest there 9 years out of 10. The best of authorities collaborated, but some may have been slightly more conservative than others. Some scatter from these causes must be expected. Other divergencies are "real," *i.e.* due to ecological conditions.

For the smaller areas we generally used actual counts, either the count in a particular year, or the average of several counts made over a period of years. In the case of "Neotoma," for instance, it was the average of 10 years of counting.

The nearctic material of Table I is graphed in Figure 1 on a semi-logarithmic basis, that is to say, areas are plotted logarithmically as abscissae, while the species-count is plotted arithmetically as ordinate.

The same material is graphed in Figure 2 on a logarithmic scale for both abscissa and ordinate. If the law of equation (3) applied, this plotting would produce a straight line and the exponent "z" could be ascertained from it.

In Fig. 3 we have plotted the first differential of the nearctic curve of Fig. 1. That is to say, plotting as abscissa the logarithm of the areas, we have plotted as ordinate, on an "arithmetical" scale, the number of species that are added at each doubling of area.

In Figures 1 and 2 we have also plotted our findings for the neotropical, which are tabulated in Table Ib and are discussed a little later.

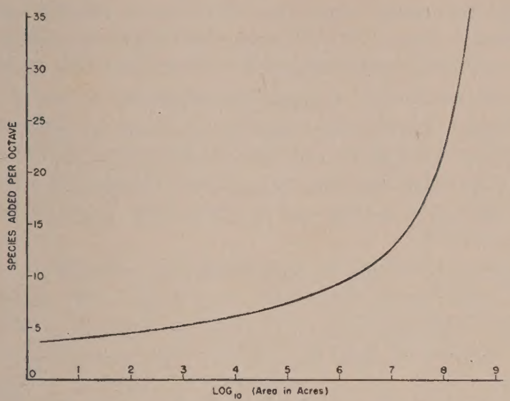

Fig. 3. First differential of Fig. 1, for the nearctic. This shows that the effect of doubling the area under study is likely to add a number of species which increases steadily as the size of area to be doubled increases.

Comments on the Nearctic Tabulations

#1 This is a suburban count, averaging about 4 species (and 4 pairs of birds) on a half acre. The count is too high to be typical of the eastern deciduous forest, though it may be typical of some suburbs, where the avifauna is impoverished in species by the elimination of those that nest at ground level, but none-the-less a high density of the remaining species is achieved. A better point could be located by a consideration of the count at Neotoma, #5 of this list. Here on an area of 69 acres the average number of pairs was 115.3 or 0.84 pairs per half acre. Since 0.84 pairs will not include more than one species, we may estimate that half an acre of eastern forest will average something like one species.

#2 This area of 6 acres is remote from even a village, in southern Butler County, Pennsylvania, but it contains Schriver's cottage and once more the count comes high, due perhaps in part to quasi-commensal species. In 1956 Schriver had 22 species on the 6 acres but over a period of years he estimates that about 18 would be the average number of species. This, like #1 above, is a very rich fauna, but again it is probably somewhat artificial.

#3 & #4 Audubon Field Notes publishes once a year a number of breeding bird counts. We have here used the reports of 1951, confining them to counts within the eastern deciduous forest area. Thirty counts were used, from Vol. 5, pp. 316 *et seqq.* We divided them into 2 groups, according to acreage. The first 26 counts relate to areas from 9 to 37 acres; the other group of 4 counts involves areas of 50 to 75 acres. Unlike counts 1 and 2, these counts, 3 and 4, appear to be on the low side, but they are, as mentioned above, an average of 30 individual counts at different places.

#5 In the Hocking Hills of south central Ohio, Dr. E. S. Thomas of Ohio State Museum has owned for many years a 69 acre tract of second-growth forest, and in 10 of those years has made a rather careful census of the breeding birds, both as regards the species present and the number of pairs of each species. The data are recorded in Table II, and, together with the information in several of the other counts where individuals as well as species were tallied, will be used below in an attempt to discriminate "sampling errors" from changes in ecology, and to estimate whether time and space act alike on the species-count.

#6 We return from Ohio and other points in the eastern forest to the Preston Laboratory grounds. This is the area reported on by Preston and Norris (1947). Since observations were fairly complete for 2 consecutive years, this count also helps with the problem of "sampling errors."

#7 Beaver County, Pennsylvania, adjoins Butler County on the east, and the State of Ohio on the west. Edeburn observed the birds on a 130 acre tract called Temple Hollow for 2 years. His figures are corrected to give a fair estimate of the number breeding in a single year. See also Edeburn (1946).

#7a Sapsucker Woods presents problems, as does #8 below, due to diversity of habitat. Dr. Allen reports an average annual count of 55 species, which puts the point well above our line, but when corrected (as nearly as we can correct it) for this diversity, the point comes quite close to the line.

#8 Beecher was not interested specifically in the species-area question, and chose a place where 2 distinct ecological assemblages adjoined. His species count is therefore high. It is possible by a reasonable argument to estimate what would be the species-count on a more homogeneous area, either the upland or the marsh, and so to obtain a point for a smaller area and a smaller species-count. This has been done on the graph and the displacement of the point indicated by an arrow.

#9 We now pass to much larger areas, and with Aretas Saunders' Birds of Quaker Run Valley we reach the last of the areas where we have a count of individuals as well as of species. Quaker Run Valley is not entirely homogeneous in its ecology, but this count is particularly useful because it is big enough to establish with fair accuracy the lognormal character of the distribution of commonness among the various species, and therefore permits a good estimate of how many species ought to be added by doubling the area, since this is essentially a case of moving the "veil-line" one octave to the left. (Preston 1948). In combination with the observed trend of the species-area curve this gives us an idea of how much change is due to the fact that we are dealing with a lognormal universe, and how much is due to an expanding universe, *i.e.* a change of ecology.

#10 to #21 These 12 are county lists, covering areas in the range from about 300 to about 1000 square miles. They are tabulations of species only. Necessarily they are subject to some uncertainties, as my authorities tend to point out. But the errors are probably not too serious and the statistical effect permits us to draw our species-area curve with some confidence among the plotted points.

#22 to #34 These involve states, or substantial portions of states, and combinations of adjoining states. We are now dealing with areas of the order of hundreds of thousands of square miles.

#35 We take the breeding-species count for the eastern U.S.A., an area of about 1½ million square miles.

#36 The nearctic is taken as including Alaska, Canada, and the United States, but excluding Greenland. We have, to a first approximation, included only the land area of the nearctic, and there is not much question that we ought to have included a considerable area of sea. For though the pelagic birds nest on land, they would not do so in the absence of sea. On the other hand it is not clear that the Greenland ice-cap or other completely ice-covered regions in the arctic have any influence on enriching the avifauna of the region. Superficially they merely have the effect of reducing the total area of the globe that is habitable by birds.

#37 In dealing with the whole earth I have used its total area, land, sea, and ice. For the scattered islands of the ocean are the breeding places of many pelagic species, and the home of many endemic species.

The Species-Area Curve for the Nearctic Birds

In Fig. 1 we plot the data of Table I, on a semi-logarithmic basis, as far as the figures for the nearctic. To plot the figure for the whole world would require the graph to be 12 times as high. In the same figure we plot also data for part of the neotropical area, *viz.,* the area around Panama. The latter may be extended smoothly to include Middle America and Mexico, at a point far above the top of the graph here given, and still further to a point representing Middle America plus the nearctic, to which point above the lower curve, nearctic plus Middle America, also smoothly converges.

The curve drawn among the points seems to represent them fairly. There is some scatter but the reason seems fairly clear. The point takes account of the effects both of sampling a lognormal distribution and of sampling areas of varying diversity of habitat. Thus Indiana and Illinois lie below the line, presumably because they are states of rather uniform habitat, while Maryland and New York lie above it, because they include high mountains, lowlands, and sea coast. Similarly Sapsucker Woods as reported by Allen and the area outside Chicago reported by Beecher lie, in their uncorrected condition, well above the line, but yield points near the line if they are supposed to have at least 2 entirely different habitats inhabited by quite different groups of species. We discuss this later under the heading of "Edge Effect."

In Fig. 1 we have drawn the tangent to the very early part of the curve, which indicates that in these areas doubling an area adds about 4.7 species. This, however, is better examined in Fig. 3. As the area gets bigger, the slope steepens, and the number of species added for each doubling of area increases.

It will be seen that the Gleason or Williams law is not obeyed by the curve in its entirety. This would call for the curve of Fig. 1 to be a straight, sloping, line. Yet it is also clear that over the range from say 10 acres to 100,000 or perhaps even 1,000,000 acres, the curve is a sufficiently close approximation to a straight line that, in the absence of information on larger areas, we should undoubtedly "graduate" it as a straight line and believe we had proved the point, that the law was true in space as well as in time, and that it held over a range of at least 4 or 5 orders of magnitude.

Now an order of magnitude, or decupling, is 3.3 octaves or doublings, so that the law is at least approximately true over a range of some 15 octaves, at least in terms of space. (Whether it is true in *time* we do not yet know). This means that the explanation which I gave of it in 1948 is inadequate. For in that paper (p. 257) the coefficient "a" of the exponent in the equation

$$n = n_0 e^{-(aR)^2} \qquad (5)$$

tends to come out consistently with a value around 0.2 and with such an exponent the substantially straight part of the integral curve (p. 274, Fig. 11) is certainly not going to extend over 15 octaves. This means that ecological assemblages are always in a state of flux with the passage of time. In the present paper, by examining the species-area curve, we see how the universe we are sampling expands in space.

Fig. 3 gives the "first derivative" of Fig. 1. Using the same scale for abscissa it plots as ordinate the number of "new species" brought in by doubling the area. When the area is about 10 to 100 acres, doubling it adds about 4 species. At 1000 acres, doubling produces about 5 new species, and at 10,000 acres it produces 6 or a little more. At 100,000 acres it produces 7½, and at a million, 9½. Beyond this the curve steepens at an astronomical rate.

In Fig. 2 we plot the same information as in Fig. 1 with logarithmic ordinates as well as logarithmic abscissae. This permits us to extend the curve to the avifauna of the whole world. The curve seems to rise very steeply from its origin at the left hand end of the graph, then to flatten for a long distance, from about 100 acres to 10^8 acres or more, and then once more to rise steeply at a slope similar to its initial one. This is to be expected, for reasons discussed later. The curve is, in a sense, sigmoid, but the tangents at the 2 ends, though parallel to each other, are not vertical lines.

THE EQUIVALENCE OF SPACE AND TIME

If time and space really are equivalent, we should be able to draw our Fig. 3 on a log-time basis instead of a log-area basis and find for various times, instead of areas, the number of new species that are introduced by doubling the time.

Causes of Change

It may be advisable to consider first the causes that produce, in a given locality, changes of fauna with the passage of time. In detail they are many, but in broad outline they seem to be 2, or perhaps 3:

(a) There is what I have called "sampling error." This may not be the best possible term, but it comes close to expressing my meaning. As the spring migration passes over western Pennsylvania a substantial proportion of the birds are newcomers that will breed for the first time. They are not returning to a place where they nested last year, but are looking for a place to settle down. Their selection is, from one point of view, a matter of chance; the early arrivals have a choice of several or many locations, and select one for reasons unknown to us, or "for no particular reason." Later arrivals, of the same or other species, may be excluded from the locations chosen by the earlier ones, since the whole locality is full, apparently, when a certain number of individuals occupy it. From our point of view the result is much the same as if we took at random a given number of individuals (or pairs of birds) from a "universe" of birds, and if we try the same experiment the next year, even if the "universe" is identical, the sample will be different. These differences I have called the "sampling error."

(b) As the years go by the habitat changes for a great variety of reasons. The forest may be buried in volcanic ash, burnt by lightning or man-made fires, or cut down for lumber or pit props. Thereafter it may regenerate through a long cycle of "ecological succession," or it may be turned into pasture, ploughed land, or suburban development. A succession of wet or dry years may change the ecological picture substantially. So may the arrival, or departure, of new predators like domestic cats or competitors like the European starling, or of new sources of food, either insects or plants. All of these and many many more factors can be grouped under the heading of ecological changes.

(c) The slow course of evolutionary change of species with time.

I think we can regard (a) and (b) as "causes" of change, but (c) is rather to be regarded as an "effect." We shall attempt to separate (a) and (b) from one another later in this paper.

Let us now return to the computation of a few examples.

TABLE II. Breeding bird censuses, Neotoma (69 acres). Compiled by Charles F. Walker and Edward S. Thomas

Species	Years									
	23	24	26	27	30	31	36	37	38	40
Turkey Vulture	1	1	0	0	0	1	0	0	0	0
Black Vulture	1	1	1	1	1	1	1	1	0	0
Sharp-shinned Hawk	1	1	0	0	0	0	0	0	0	0
Ruffed Grouse	0	0	0	0	0	1	0	0	1	0
Mourning Dove	1	2	1	4	2	2	2	2	4	2
Yellow-billed Cuckoo	0	0	2	1	1	1	1	0	1	1
Black-billed Cuckoo	0	1	0	2	1	2	1	1	1	1
Screech Owl	0	0	0	0	0	0	1	0	1	0
Horned Owl	0	0	1	0	0	0	0	0	1	1
Whip-poor-will	8	8	8	7	5	5	3	3	4	2
Hummingbird	1	5	1	2	2	1	3	1	2	2
Flicker	2	1	0	1	0	1	0	0	1	0
Pileated Woodpecker	0	0	0	0	0	0	1	0	1	0
Red-bellied Woodpecker	1	0	0	0	0	0	0	0	0	0
Hairy Woodpecker	0	1	1	0	0	0	2	0	1	1
Downy Woodpecker	1	1	0	1	1	1	1	2	1	1
Crested Flycatcher	3	2	1	1	2	1	2	1	2	2
Phoebe	7	4	3	5	4	4	5	6	4	3
Acadian Flycatcher	3	6	5	5	5	3	5	8	8	10
Wood Pewee	2	4	2	2	2	2	2	0	1	1
Blue Jay	1	0	0	0	0	0	1	0	0	0
Crow	0	0	1	0	1	1	1	1	0	1
Carolina Chickadee	1	2	3	2	1	4	1	1	3	3
Tufted Titmouse	2	2	2	2	1	1	2	1	4	2
White-breasted Nuthatch	1	1	2	1	1	1	1	1	2	1
Bewick's Wren	1	0	1	0	0	0	1	1	0	0
Carolina Wren	4	7	0	1	1	2	0	0	0	0
Catbird	1	1	1	0	0	0	0	0	0	0
Robin	1	1	0	3	1	0	1	1	1	1
Wood Thrush	7	5	4	2	2	2	4	2	3	3
Bluebird	1	2	2	2	1	0	0	0	1	1
Gnatcatcher	1	2	2	1	3	3	2	1	2	2
White-eyed Vireo	4	3	4	2	3	2	1	1	0	0
Yellow-throated Vireo	1	1	0	1	0	1	0	0	1	1
Red-eyed Vireo	8	10	9	7	7	11	14	16	13	18
Black & White Warbler	3	2	4	1	3	2	3	1	5	4
Worm-eating Warbler	4	3	6	3	4	6	7	7	7	7
Blue-winged Warbler	3	4	2	2	2	1	1	2	1	1
Yellow Warbler	0	1	0	0	0	0	0	0	0	0
Cerulean Warbler	4	3	3	2	1	2	2	2	2	4
Prairie Warbler	5	4	2	2	1	1	1	1	1	1
Ovenbird	3	7	3	2	2	9	5	5	11	6
Louisiana Water-thrush	4	3	3	1	1	1	1	1	1	2
Kentucky Warbler	1	3	2	0	2	0	1	2	2	2
Northern Yellowthroat	1	1	1	1	0	0	1	1	1	0
Chat	12	7	6	6	6	4	2	2	1	2
Hooded Warbler	4	4	6	1	2	2	1	1	1	0
English Sparrow	0	0	0	0	0	0	0	0	1	0
Cowbird	P	P	P	P	P	P	P	P	P	P
Scarlet Tanager	4	4	4	2	2	3	2	2	3	4
Summer Tanager	3	3	3	3	1	1	1	2	3	1
Cardinal	5	3	7	5	3	3	3	3	5	5
Indigo Bunting	6	5	3	4	4	2	2	5	2	4
Towhee	3	4	8	6	5	5	2	3	4	2
Chipping Sparrow	2	2	1	2	2	2	1	2	2	3
Field Sparrow	8	6	9	7	7	5	2	2	3	3
Song Sparrow	2	1	3	1	1	1	0	0	1	0
TOTAL SPECIES	47	47	42	42	41	42	44	38	46	39
TOTAL PAIRS	143	146	133	107	97	104	97	95	120	111

Neotoma

In Table II we give Dr. Thomas' tabulation of the species and individuals (pairs) breeding at Neotoma over a period of 18 years. Unfortunately, in only 10 years out of the 18 was a complete accounting made, and this complicates our figuring. We can however make an approximate estimate of what was going on.

Restricting ourselves to the 5 pairs of consecutive years, 1923-24, 1926-27, 1930-31, 1936-37, and 1937-38, we find that the species present in the 2nd year of the pair, but absent in the first, number 3, 6, 4, 0, and 12 respectively, while the species present in the first year and missing in the 2nd amount to 3, 6, 3, 6, and 4. The average of these 10 changes is 4.7. If we take the 10 years observed as being equivalent to consecutive years, and observe that in the 10 years 57 species were seen, while the average was only 42.8, for an increase of 14.2, then since $10 = 2^{3.3}$, the effect of doubling the period of observation is to increase the count of species by $14.2/3.3 = 4.3$. This estimate is probably a little higher than if the years had been strictly consecutive. Still another way of looking at it is this: In the 10 years that were actually sampled, there were 3 species that appeared only once, and in each case they were represented by a single pair. It is reasonable to assume that if we had the counts for the missing 8 years, we should have found about 3 more species that appeared only once. This would make a total count of species of 60 in 18 years, up 17.2 from the average number of 42.8. Now 18 is $2^{4.17}$, and so 4.17 is the number of doublings available to us. Then $17.2/4.17 = 4.12$, which is the number of "new" species added by doubling the *time* of observation. By these 3 methods then we have estimates of 4.7, 4.3, and 4.12, as the number of species added by doubling *time,* on an area of 69 acres. The average of these 3 figures is **4.47.**

Referring now to Fig. 1 or, better, to Fig. 3, and noting that log 10^{69} is 1.84, we find that the effect of doubling the *area* is to add 4.3 species. The agreement seems to be almost exact.

Note that at Neotoma the ecological set-up was not static; the forest was growing up over those 18 years. The change therefore includes both "sampling error" and change of habitat. Some species definitely tended to become more common or regular and others to become less so. In including both effects, the change with time is similar to the change with area.

The Preston Frith

The Preston Laboratory Grounds, or Frith, have an area of about 90 acres. Preston and Norris (1947) give the breeding species of 1944 as 42, including the Cowbird. From 1944 to 1958 inclusive the count has risen to 61, an increase of 19 over a period of 15 years, which is 3.9 doublings. This is an increment of 4.87 species per doubling in *time*. From Fig. 3 we should expect about 4.7 for a doubling in *space*. Again the agreement is good.

The matter may be tested more directly and without reference to Fig. 3. The Pennsylvania Manual gives the area of Butler County as 794 square miles or 510,000 acres, which is 5,700 times the area of the Preston Laboratory Grounds (c. 90 acres "inside the fence"). Now $5{,}700 = 2^{12.5}$, or 12.5 doublings. The man who today probably knows the avifauna of Butler County better than anyone else is Mr. Hal H. Harrison, who lives just beyond its margin and travels about it a great deal. His estimate is that there are 99 regular breeders in the County, while Norris found 42 or 43 annually on the Laboratory Grounds. Now $99-42 = 57$ and $57/12.5 = 4.6$ species per doubling of area. Though Harrison's list is longer than mine (he knows the outlying parts of the County better than I do), I know of one or 2 regular species about which he is doubtful, and this would bring the tally to 4.7 per doubling. In any one year we can expect at least a few irregular species to breed, so the tally will run a little higher, agreeing in space almost exactly with the calculation for time. It may be noted that if Butler County were average, *i.e.* if it fell exactly on our line, it should have about 113 regular breeders, but to the best of our knowledge it falls well below this level, as does the neighboring Beaver County as estimated by Todd.

Sapsucker Woods

Sapsucker Woods, near Ithaca, New York, affords another opportunity to check space against time, for records have been conscientiously kept and observations go back for 50 years. The situation is a little complicated because the 150 acres of the woods consist of 120 acres of woodland, 10 of water, and about 20 of bushy fields. This variety tends to make the species count high. On 120 acres of woodland we should, from our graph, expect about 34 species: Dr. Allen reports that over a period of 50 years some 59 species have nested in the wooded area, though only 36 are true woodland species.

Let us begin however by lumping the whole area together. On the 150 acres, in the years 1957, 1958, and 1959, there nested 57, 51, and 58 species, for an average of 55. In the course of 50 years, 84 species have been recorded as nesting on the area or 29 more than the average for a single year. Now 50 years $\doteq 2^{5.6}$ or 5.6 doublings, and $29/5.6 = 5.2$ for each doubling of time at Sapsucker Woods, which is not far from the figures we find elsewhere, though a little higher, probably because of the 10 acres of water.

Dr. Allen notes that in the Cayuga Lake basin, of which Sapsucker Woods is a part, 156 species have been known to nest. The area of the basin is about 1600 square miles or 1.02 x 10^6 acres. On such an acreage, our curve (Fig. 1) predicts about 123 regularly breeding species. (The number in a single year may be slightly higher since some irregular ones may be present each year). Therefore 156 − 123 = 33 species, and if we assume that something like a hundred years accumulated this excess, then since $100 = 2^{6.6}$ or 6.6 doublings, we have 33/6.6 = 5.0 species for each doubling of time on the Cayuga Lake basin.

We may now test also for the effect of area, as well as time:

The area of Cayuga Lake Basin is $2^{12.7}$ times the 150 acres of Sapsucker Woods. The number of species nesting in the basin was 156, and I assumed this was for 100 years. In 50 years it should be about 151. The number nesting in Sapsucker Woods over a period of 50 years is 84, as mentioned above, and 151 − 84 = 67 species. Then 67/12.7 gives 5.3 species for each doubling of area in this locality. This is quite similar to the figure for doubling of time, as in the previous paragraph.

We thus have 3 figures as follows:

On doubling time at Sapsucker Woods, we add about 5.2 species.

On doubling time over Cayuga Lake Basin, we add about 5.0 species.

On doubling area in this locality, we add about 5.3 species.

Note that in the absence of an actual count for the Basin in a single year, we had to use our curve to get the figure of 123 "regular" species. This, however, is probably not far out, for Dr. Benton (our point 19) gives the count for Cayuga County as 122, and the area of this county is 0.63 times the area of the Basin, so the Basin would be expected to have about 127 or 128, and this is close enough.

The Avifauna of States

When we get to larger areas, such as states, the number of species that are irregular, sporadic, or doubtful, is probably not nearly so well known. In correspondence, Val Nolan, Jr. gives the number for Indiana as 18, Traylor gives about a dozen for Illinois, Todd gives 14 for western Pennsylvania. Yet quite a number of species might once in a while be represented by a single pair in any state and escape notice. Thus I think it possible that in the course of 50 or 100 years, 30 species might nest once or more but be missing in at least 5 or 10 years. This would produce about the same figure, 4 or 5 per doubling, we find for the smaller areas of Neotoma and the Frith. This means that if we converted our abscissae in Fig. 3 from an area to a time basis, a year would fall at some point not very far from the lefthand end of the curve. We cannot locate the point with any real accuracy because the curve here is too flat. The right-hand end would be more useful, and this takes us far outside the records of history and we must have recourse to the fossil record.

The Fossil Record

In correspondence, Dr. Wetmore informs me that few of our modern species of birds appear to go back beyond the Pliocene. He writes, "It is my personal conclusion that the existing species of birds had their period of evolution into their present form in the latter part of the Tertiary, presumably during the Pliocene, so that they were definitely established as distinct entities at the beginning of the Pleistocene or Ice Age. Some, the song sparrows for example, have apparently had continued evolutionary change as marked by the numerous subspecies now evident. Others were already stabilized and did not show such changes." (See also Wetmore 1959).

Brodkorb (1958) concurs: "As far as identifiable, all *genera* in this (Middle Pliocene) avifauna occur in the present avifauna of Oregon, but the *species* are extinct, whereas the Upper Pliocene avifauna contains a large proportion of living species. This affords additional evidence that living species of birds have a time span extending no further back than the Upper Pliocene." (Brodkorb 1955). (The italics are mine and I have rephrased the statement slightly). In other words, if we sample our birds now, and had sampled them some 4 or 5 million years ago, we should have practically no species common to the 2 samples. This is what happens with the passage of time. When does the same thing happen with increase in space? By referring to Fig. 2 we see that it really happens at the total area of the whole world, where the curve from both the nearctic and neotropical origins become tangential to the limiting tangent. We might say the curves are substantially parallel to this tangent at $10^{9.5}$ or $10^{10.5}$ acres.

Thus 4 or 5 million years, or $10^{6.5}$ to $10^{6.7}$ years, are equivalent to some $10^{9.5}$ or $10^{10.5}$ acres, and so a year is equivalent to something like 1000 acres or 10,000 acres, or say one to ten square miles.

On this basis the area that we can compare from year to year, that is, on a basis of 1, 2, 4, 8 years, etc. is 1000 acres or a little more, and here doubling the area should produce about 5 or 6 "new" species. Similarly, counting for 2 seasons instead of one should produce about 5 or 6 new species. This seems likely to be nearly enough correct.

The evidence suggests that time and space are in fact essentially equivalent or at least that there is a strong resemblance.

SEPARATING THE EFFECTS OF "SAMPLING ERROR" FROM THE EFFECTS OF CHANGING ECOLOGY

Confining our attention to the nearctic, for which our information is more complete, we can obtain from Fig. 1 the number of species of breeding birds to be expected on an area of given size, and from Fig. 3 we can obtain the number of species we may expect to add by doubling the area. Then dividing the second figure by the first and multiplying by 100, we can obtain the percentage increase in species. This percentage for a number of different sized areas is plotted on Figure 4 (upper curve).

From about a thousand acres to a hundred million acres this percentage increase is around 8 or 10%. This percentage figure is similar for nearctic and neotropical regions.

However, it consists of 2 components. There is first the "sampling error," which is the big element with very small samples; and, second, there is the inevitable change of ecological set-up and diversity of habitat when we come to large areas.

Now it appears that the sampling error is always about 3 or 4 species per doubling. At Quaker Run the lognormal curve shows that doubling the sample would theoretically increase the species by about 4½. In the very much smaller

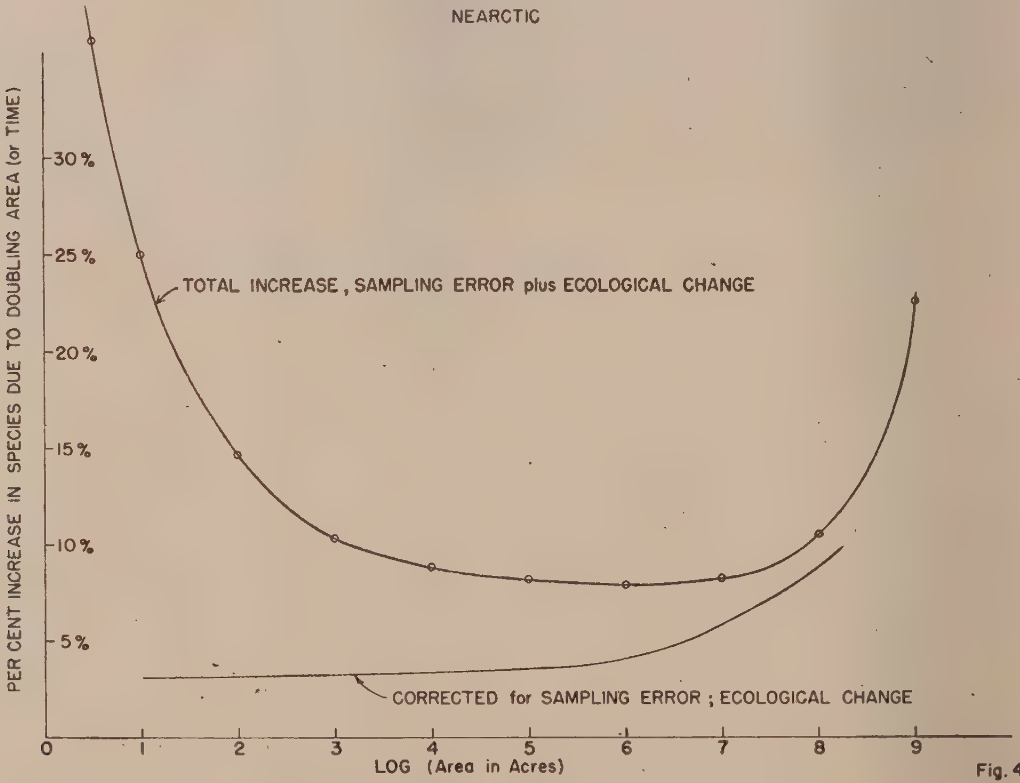

FIG. 4. Increase in species of breeding birds due to doubling area or time, expressed as a percentage of the species before doubling. The upper curve is the percentage increase actually observed, and is compounded of the "sampling error," due to the fact that 2 equal, random, samples of a lognormal population are likely to differ substantially in the species they produce, especially with small areas and hence small samples, and of the effect of ecological change, which becomes increasingly important with large areas. The lower curve subtracts the sampling error and gives an estimate of the increase in species due solely to ecological change, or diversity, as we increase the area (or elapsed time).

areas of Neotoma and Preston Frith, where doubling takes the form of doubling time and not space, the evidence is that the figure is again close to 4. The state counts indicate that it is still no greater than 4, and may be a little less, our judgment once more being based on doubling time; that is, we take account of sporadic or occasional or intermittent breeders. Finally, when we come to the bird population of the whole world, and note that most species try to breed at least once every year, we can agree that we are not likely to add more than 4 species by using a 2 year count instead of one.

Thus to a first approximation we can probably agree that over an immense range of area and of time, doubling our sample is likely to produce an increment of species due to what we have called the sampling error, as distinct from the variation arising from changing ecology, not far from 3 or 4 species, no matter what the size of the area.

But 3 or 4 species is a much larger percentage of the total species in small areas than in large.

If we deduct this percentage from the upper curve of Fig. 4, we are left with the lower curve thereof as representing the increment due to changing ecology. This curve is virtually flat at about 3½% over a very wide range.

Some Special Problems

Before we leave the nearctic and its avifauna, a few comments by way of explanation may be useful on two or three points.

The Initial Steep Rise of Fig. 2

It can be shown that if the complete population of an area such as an isolated island or a quasi-isolate such as the eastern deciduous forest conforms to a complete lognormal distribution, then a small sample will be abnormally rich in species in proportion to the number of individuals. This would be true if it were a strictly random sample, and thus when we collect a small sample or study a small area, we find our collection growing "richer" in species, at an abnormal rate. In the case of territorial birds, the "enrichment" is even faster, and both these factors tend to make the early part of the curve too steep. An opposite effect can be expected with flocking birds in winter, or colonially-nesting birds, or with most plant quadrats, since most plants are more or less clumped or "contagiously distributed."

The "Edge Effect"

It is commonly stated that birds are more plentiful at an ecotone, or the margin of a habitat, where it adjoins another habitat, than they are in the middle of a habitat; for instance, they are more plentiful at the edge of a wood than in its interior. The same thing has been urged for mammals, especially big game. It has been argued that they may depend on the one habitat for shelter and the other for food, or that their requirements are better met by the resources of 2 habitats than of one. This is called the "Edge Effect" but whether it is a genuine effect, causing individuals to concentrate at the ecotone, or whether it is merely an appearance, due to an enrichment of species to be seen at the margin, I am not completely sure. The problem does concern us a little, however, in the present paper, because the points that fall appreciably above our curve do so mainly because of an enrichment in species due to the presence of more than one kind of habitat, *i.e.* to the presence of an important "ecotone."

Suppose we take a wooden frame in the form of a square, intended to delimit a quadrat of 150 acres, and drop it at random upon an area of uniform climax forest in our deciduous eastern forest country. Then by reference to our species-area curve, Fig. 1, we should expect it to enclose about 37 species of breeding birds. If we now drop it somewhere else, not far away, on a similar area, we should again expect about 37 species, though several of these species might be ones that we did not net at the first drop. This is the inevitable consequence of sampling a lognormal population, with some species sufficiently uncommon that we cannot expect to net even a single pair in a 150 acre quadrat.

Now let us suppose that adjoining this climax forest we have a large area of open marsh. This might be just as thickly populated with birds as the forest, and if we dropped our frame on it we might again net 37 species, and quite conceivably not one of them would be a species that breeds in the forest.

But if the ecotone between marsh and forest is sharp, and sometimes it is, we might drop our frame so that it included 75 acres of forest and 75 of marsh. Then, referring once more to our species-area-curve, we should expect to net 32 species of forest birds and 32 of the marsh, for a total of 64 species. This is 72% more than if we drop the net on a single habitat clear of the ecotone.

Sapsucker Woods is an area of 150 acres where Dr. A. A. Allen has long kept track of the breeding species, and he has provided me with a list of them. Those found in a single year averaged 55 species, which seemed excessively high. In our discussion of the subject, it soon became clear that it was the presence of two distinct habitats, forest and open marsh, that was producing the result. The computation made above, therefore, is not entirely hypothetical; it is a rough approximation to the Sapsucker Woods situation.

When the corrections are made, Sapsucker Woods falls nearer to the curve (Fig. 1) than do Neotoma or Preston Frith, though they are not nearly so far off as Sapsucker Woods was in the uncorrected form. The reason they are not exactly on the line may be that they are not strictly homogeneous habitat, a point on which Norris (1947) comments in the case of the Frith. Similarly, Saunders comments that Quaker Run Valley is not homogeneous, and probably for this reason his point also lies above the curve, though at no great distance from it.

Beecher's 482 acre area near Fox Lake, Illinois, is also highly heterogeneous. He recognizes 4 distinct habitats, but it is probable the birds recognize fewer, perhaps only 2. If these 2 were equal in size and equally well populated, then, instead of reporting 72 species on 482 acres, he would report 36 species on 241. If we assume this is as good a correction as we can make in so complicated a situation, the new point, 36 on 241 acres, falls almost exactly on the line, though the original point falls far above it.

When our quadrat reaches the size of a county, several hundred square miles instead of a hundred or a few hundred acres, or the size of a state, some scores of thousands of square miles, we must expect that the random dropping of the net will include a variety of habitats, and so we must necessarily get composite samples representing 2, or several, populations of birds. Thus the curve will tend to climb above the initial tangent. The points will be scattered somewhat, some climbing higher than others, according to the diversity of habitats in the various counties or states. We no longer attempt to correct for this, but obtain as best we can a representative sample of counties and states, plot the points, and draw the curve through the middle of them.

The properties of the palaearctic avifauna may be expected to be similar to those of the nearctic, but the palaearctic is much larger in area and has many more species of breeding birds. De Beaufort (1951) credits it with 1110 species; I estimate the area to be about 1.22×10^{10} acres. This area is plotted at P in Fig. 2, on the nearctic curve, where it corresponds to an avifauna of 1090 species, very close to de Beaufort's figure. In other words, if the nearctic were as big in area as the palaearctic, it would most likely have as many species as the palaearctic now has. The inference seems to be that if we had a complete species-area curve for the palaearctic, beginning in a region as similar as possible to the eastern deciduous forest, the curve could be superimposed on the nearctic curve and would fit it exactly.

The situation with the neotropical avifauna is different, and merits a slightly larger discussion.

THE NEOTROPICAL AVIFAUNA

It will be interesting to see if we should reach somewhat similar conclusions by starting our investigations in a totally different environment, and so I have attempted to outline what happens in the neotropical forest. Here we are naturally even worse off for authentic information. I have had to rely heavily on just 2 or 3 authorities, Sturgis (1928), Eisenmann (1952 and 1955) and Irby Davis (1952, 1953, and 1955). The information is tabulated in Table I, and graphed in Figs. 1 and 2.

Comments on the Tabulation

I could find no information on the number of pairs or of species in strictly small areas in Panama, whence most of the other figures came. I used some of Davis' results of tropical lowland and rain forest in Vera Cruz State, Mexico. The points seem to lie above the expected level, ranging from 84 to 106 species when we might expect 55 or 60. The reason is not clear. We have also some information from Dr. Skutch in southeastern Costa Rica. In a letter dated December 1, 1958 he says of his home area at Quizzara, southeastern (Pacific coast of) Costa Rica, 2500 ft above sea level, in the 12 months September 1, 1943 to August 31, 1944, on 3.75 acres:

"Species counted as resident, 33: individuals counted as resident, 110: density, 29.3 breeding birds per acre: nests found with eggs, 83. Many of the resident birds foraged beyond this area in the neighboring woods and thickets. I believe I had a rather unusual concentration of breeding birds about my house at that time."

#B5 Barro Colorado Island, in the Panama Canal. Eisenmann (1952, p. 3) says that though we have positive evidence of the breeding of only about 100 species, it is probable that about 200 breed *more or less* regularly on the Island. (Italics mine). Since we are concerned with those that breed *quite* regularly, I thought 150 to 160 might be a fair estimate.

#B6 The Panama Canal Zone itself has an area of about 500 square miles. Sturgis (1928, pp. XII and XIII) estimates that if we include a modest amount of contiguous territory that is not politically in the Zone,

we should meet about 434 species of birds of which 21% do not breed there, so that 343 species do. The area of the contiguous territory she does not specify. I have assumed that it may be as large as the "political" part of the Zone, giving a total area of about 1000 square miles or 600,000 acres. Clearly we are making a lot of assumptions and must end with only a rough approximation.

#B7 Take next the Republic of Panama whose area is about 28,575 square miles or 1.83×10^7 acres. Using Eisenmann's (1955) list of Central American birds, it appears that about 680 species breed within the Republic of Panama. An indirect estimate from Sturgis (1928) gave roughly 700. The agreement is good.

#B8 Passing outside Panama to the west and north, we can check the species in Eisenmann (1955) that breed in Middle America from Panama to Mexico inclusive: these aparently total about 1180 species, while the area of the countries, from other sources, appears to be about 985,000 square miles or 6.3×10^8 acres. There is a good deal of sea coast to Middle America, and once more we face the problem of how much sea we ought to include. Since this problem is insoluble, we have used simply the land area. This might justify us in reducing the total species count by the number of pelagic species. But these are only a small fraction of the total of 1180.

#B9 We have now brought the nearctic and neotropical into contact at the Mexico-U.S.A. border and may add either A to B or B to A. In either case we finish with an area of 4.13×10^9 acres. From Eisenmann's 1955 list it appears that species that breed in both nearctic and Middle America number about 303, so that the total breeding species of the 2 combined areas is $625 + 1181 - 303 = 1503$.

When this point is plotted on an extension of Fig. 1, it lies very neatly on both curves, each of which is virtually straight, with this sort of plotting, above the level of 600 species. When it is plotted by the log-log method of Fig. 2, it lies neatly on the neotropical curve as this proceeds on its way to the final point, the birds of the world. It does not fit so well on the nearctic curve, since the relatively small area added by Middle America produces such an enormous increase of species. The nearctic curve does however head reasonably well for the ultimate point, birds of the world.

From Davis' figures it appears probable that on a single acre of neotropical lowland forest we may get as many as 7 species of birds nesting. But whether the figure is 1, 7, or 14, it will make little difference to the general shape of the species-area curve in Fig. 1. A smooth curve can be drawn readily through all the points of Fig. 1, except those for the 15 acre counts, and it continues smoothly through two other points on the extension upwards of Fig. 1, *e.g.* the points corresponding to B8 and B9.

When we plot by the log-log method, as in Fig. 2, we find once more that there is a long stretch of the curve that is virtually straight, from an area of 1000 acres or less to an area that takes in all Middle America, almost to 10^9 acres. The equation of this straight line is approximately

$$S = 40 \sqrt[6]{A} \qquad (8)$$

More observational information might modify it somewhat. It is subject to greater uncertainties than the equation for the Eastern deciduous forest.

Comparative Density of Species and Individuals in Neotropical and Nearctic

In Fig. 1 the curves for the neotropical forest and the eastern deciduous forest have an interesting property. From their origin at about one acre to areas of 10^5 acres the neotropical curve lies at just about 2.55 times the height of the other. In other words the neotropical forest contains 2½ times as many species as an equal area of eastern deciduous forest. For areas greater than 10^5 acres the factor is somewhat higher than 2½, rising in fact to a little over 4. The reason for this increase is not clear, though it is probably real. One possibility is the presence of larger numbers of endemics, species of relatively local distribution, in the neotropical, but I am not sure that this is sufficient to account for the whole of the increase.

Apart from the increase to 4⅓, the general level in smaller areas of 2½ times the eastern deciduous forest population carries some interesting implications. I have heard it said that in the neotropical forest, though the avifauna is much richer in species, it is not richer in individuals. If our curves are both correctly drawn, this does not seem possible. For the upper curve looks as though it maintains its relative altitude down to the smallest areas, and this seems to be confirmed by Irby Davis' figures. Even down to a one acre quadrat we seem to have 2½ times as many species, and we must therefore have 2½ times as many individuals. (Davis' figures would set the ratio as 4.1 rather than 2.5).

The discrepancy in richness of species appears more spectacular if we express it, not as the number of species on equal areas of neotropical and nearctic terrain, but as the areas of the 2 terrains that contain equal numbers of species. If our curves are correct, we can find 100 species breeding on 200 acres of neotropical landscape, while it takes 200,000 acres of eastern deciduous forest to run up the same total. Two hundred species can be found on 300 square miles of neotropical land, but it takes 70,000 square miles to provide that number in the nearctic.

The discrepancy in number of individuals is also a matter of interest. The boundary between nearctic and neotropical is drawn somewhat differently by different authorities, but according to one delineation the neotropical area in its entirety is some 30% bigger in area than the nearctic, though some of it is not tropical. However, the great bulk of its lies in warm zones, contrary to the state of affairs in the nearctic. Thus it seems likely that the neotropical may contain 1.3 x 2.5 = 3¼ times as many individual birds as the nearctic.

At a recent symposium of the A.O.U. at Cape May, New Jersey, the question was raised as to whether the tremendous influx of northern birds into South America, during the northern winter, might not depress the population of neotropical species. But if *all* the birds of the nearctic went south of the Rio Grande for the winter, it would raise the density of birds there by only 30%. In practice a large proportion remain north of the Rio Grande, so the increase in density in the neotropical is probably no more than 10%. Even if it is 20%, it is still much less of a population pressure than results from the fledging of the young of the neotropical species themselves.

On the high plateau of Mexico in Jalisco near Guadalajara, I estimated that probably more than 75% of the (individual) birds were wintering northerners, but at San Blas in Nayarit, at sea level, it seemed likely that less than 25% were from the north. Sr. Miguel del Toro tells me that in Chiapas, southern Mexico, in the central part of the State, where the cover is deciduous forest, about 50% of the birds in midwinter are from the north, but in the humid regions it falls to 25% or less. Dr. Alexander Skutch writes that in the tropic forest in Costa Rica, at San Isidro del General, there is only one wintering northerner near ground level, the Kentucky Warbler, and this is a quite negligible proportion of the whole; in more open country, where there is some cultivation, the proportion may rise to as much as 20%. He adds that in Honduras and Guatemala the proportion would be considerably higher than this. In Panama it seemed to me that in the forest the proportion of northerners was negligible, but in the swamps and by the sea it might be appreciable, though perhaps not high.

Dr. Alden H. Miller reports on his experience in Columbia:

> "particularly in the subtropical forests at the 6,000 foot level, there were three species of North American birds that were quite common right through the winter, namely, the Blackburnian Warbler, Canada Warbler, and the Swainson Thrush. We did have occasional individuals of other species, and at times in the first part of the fall migration rather considerable numbers of Wood Pewees. Through the winter also were a few Acadian Flycatchers.
>
> "I have tried to recall how often I encountered these species, particularly the two abundant warblers. I would say that in the aggregate they do not represent more than ten per cent of the individuals seen as one works through the subtropical forests. This, as you will recognize, is truly a rough estimate."

Thus in the forest regions of South America proper, the pressure exerted by wintering northerners would seem likely to be trifling.

The Probable Lognormal Distribution of Neotropical Birds

The number of species of birds breeding in the nearctic is about 625. The number in the neotropical is 2500 (de Beaufort 1951). The ratio is 4 to 1. We have estimated that perhaps the number of individuals is in the ratio of 3¼ to 1. It seems to follow that on the average a neotropical species is represented by about as many individuals as is a nearctic one. We have reason to believe that the nearctic population is distributed lognormally among its species, according to the formula

$$N = N_0 e^{-(aR)^2}$$

where $N_0 = 65$ and $a = 0.19$ (Preston 1948, p. 281)

It would seem that a first approximation to the distribution of neotropical birds might be given by

$$N = (pN_0)e^{-(aR)^2} \text{ or } N = 4\ N_0 e^{-(0.19R)^2}$$

At least it seems likely that the constant "a" is not far from 0.2, a thing we have found to be true for a great many biological populations. This, however, I hope to discuss from another point of view in a later paper.

Relative Rates of Evolution in the Neotropical and Eastern Deciduous Forest

The slope of our curves (Fig. 1) is $dN/d(\log A) = A\ dN/dA$ and we have seen that for a given value of A this slope is some 2½ to 4 times as steep in the neotropical forest as it is in the eastern United States. If we can safely draw the analogy between time and space, we should have $t\ dN/dt$ some 2½ to 4 times as steep for a given interval of time (t). In other words it suggests that evolution (of birds) proceeds several times as fast in the tropics as in the temperate zone.

This has been suspected by others, not simply for birds but for forest trees and other groups. Indeed it has been suggested that the tropical rainforest is a sort of nursery where species are raised and from which they are sent out to populate the temperate regions. Our argument in this paper does not prove the point, but it suggests it and would be consistent with such a supposition.

Cause and Effect

It is not difficult to concede that the organisms of two continents differ because they have not shared too closely their evolutionary history. This was Darwin's conclusion during the voyage of the Beagle. It is also a point made by Williams. This allocates the cause to time and the effect is found in space. Since space and time are coexistent, it seems philosophically unlikely that cause is limited to one and effect to the other. Indeed we are all aware that the effect, the change of species, is seen in time as well as in space. We might also argue that the driving force of evolution, as of history, arises from the fact that at any one time things are different in one place and in another. Sooner or later, and usually continuously, this produces an interaction which is visible both as an effect in time and as an effect in space. In the absence of variations from place to place, it seems likely, or at least possible, that the tempo of evolution in time would decline to zero.

Acknowledgments

I am indebted to very many men for information on the nesting species in the areas, counties, or states with which they are most familiar; their help is acknowledged at the appropriate point in the text. I am indebted to Dr. Edward S. Thomas for reading the text in substantially its present form. One or two other friends have seen the text and read it (not necessarily critically, but helpfully) in an earlier version, among them Dr. C. B. Williams, and his interest too I wish to acknowledge. I have received a good deal of help from Mr. R. R. Lehnerd of Preston Laboratories, Inc. in preparing the figures, and from my secretaries, Mrs. Bertha J. Povlick and Miss Marjorie L. Swallop, in typing and retyping, and in calculating and computing and recomputing, and from Mr. Russell Southwick of these laboratories in proof-reading and checking computations.

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LONG-TERM ECOLOGICAL STUDY IN THE OAK RIDGE AREA: III. THE ORIBATID MITE FAUNA IN PINE LITTER[1]

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Introduction

Oribatid mites are abundant in many soil and litter situations. While it would appear that they play a role in the decomposition of leaf litter, their importance in soil formation has not been evaluated (Murphy 1955). Details of bionomics and ecology are known for only a few of the species. Most oribatids are thought to be feeders on fungus, but some ingest raw or undecomposed litter (Spencer 1951), and others burrow into pine needles (Jacot 1939). Much taxonomic work remains to be done on the American fauna, and proper identification of the immature stages is virtually impossible. Very little is known of the distribution and abundance of these mites in American soils.

The purposes of this study were to investigate the abundances of the various oribatid species found in litter of pines (*Pinus echinata* Miller and *P. virginiana* Miller) and to examine local variation in numbers for these mites, both between and within similar stands of trees. Other arthropod groups were treated similarly but in less detail. Such data on the structure and variation of the litter oribatid fauna are necessary prerequisites to studies of the importance of the litter fauna in the soil ecosystem.

We are grateful to Dr. S. I. Auerbach, Health Physics Division, Oak Ridge National Laboratory, for aid and advice during the course of this study, and to Dr. Marvin Kastenbaum, Mathematics Panel, Oak Ridge National Laboratory, for guidance in the analysis of the oribatid mite data. Identifications of arthropod species were kindly provided by the following specialists:

Coleoptera: Dr. Henry F. Howden, Science Service, Department of Agriculture (Ottawa, Canada, and Dr. M. W. Sanderson, Illinois State Natural History Survey. Thysanoptera: Dr. L. J. Stannard, Illinois State Natural History Survey. Hymenoptera: Dr. A. C. Cole, University of Tennessee, and Dr. C. F. W. Muesebeck, U. S. National Museum. Diptera: Drs. P. H. Arnaud, R. H. Foote, C. W. Sabrosky, and A. Stone, U. S. National Museum. Araneae: Dr. W. J. Gertsch, American Museum of Natural History. Oribatei: Dr. T. A. Woolley, Colorado State University. Pseudoscorpionida: Dr. C. Clayton Hoff, University of New Mexico. Pauropoda: Dr. P. A. Remy, Faculte des Sciences de Nancy (Nancy, France).

Materials and Methods

The pine stands investigated are located in Melton Valley, which is part of the AEC Controlled Reservation in Anderson and Roane Counties, Tennessee. The valley has a topography typical of the Ridge and Valley Province of the eastern part of the state; it consists of approximatley 5 square miles of woodland and old fields (abandoned for at least 15 years) lying between Haw and Copper Ridges (Bethel Valley Quadrangle of the U. S. Geological Survey). In Melton Valley, deciduous trees occur on the tops of the ridges and in some areas of the valley. The old field sites and some of the slopes support both short-leaf pines (*P. echinata*) and scrub pines (*P. virginiana*). Typically, these pine stands contain various herbs and shrubs, lichen pads, and occasional clumps of moss.

Three pine stands of similar topography and plant cover were selected for study. Sites which were similar in all aspects were not found; there were recognizable differences in these 3 areas with respect to abundances of *P. echinata* and *P. virginiana*, the degree of canopy closure, and density and composition of the herb and shrub strata. However, the depth and make-up of the forest floor debris were similar in the areas.

Three permanent collecting stations were laid out in each of the areas. Areas were designated as I-III and stations as A-I, with Area I containing stations A-C, Area II containing stations D-F, and Area III containing G-I (Table VI). A station was 63 cm square, and divisible into 225 units, each of which corresponded to the diameter (4.2 cm) of the sampling tool. Three samples were taken from random positions on a grid on the same morning in each of the 9 stations starting June 29, 1956, and continuing at weekly intervals until August 17, 1956. Nine samples per area for 8 weeks made a total of 216 litter samples. Each sample covered 13.9 sq cm. Thus, nearly 3000 sq cm (30% of a square meter) of forest floor cover was examined in the samples. In each station, 8% of the surface area was removed by sampling.

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[1] This research was conducted in the Health Physics Division of the Oak Ridge National Laboratory, operated for the U. S. Atomic Energy Commission by Union Carbide Corporation, Oak Ridge, Tennessee.

[2] Summer Research Participant with Oak Ridge Institute of Nuclear Studies, Health Physics Division, Oak Ridge National Laboratory (1956-1957).

Collecting was done with a steel core tool fitted with a plastic insert as a sample container (Auerbach and Crossley 1960). The plastic insert containing the sample was placed undisturbed, with the litter profile in reverse, into a Tullgren funnel. The funnels were in an environment-controlled laboratory with a temperature of 70°F, and a relative humidity of 50%. A 40-watt bulb was used over the Tullgren funnel. During the week of extraction, the temperature varied from 90-100°F on the surface of the sample. Arthropods were collected in an attached weighing dish which contained 80% alcohol.

The arthropods in the weighing dish were identified and counted with a wide-field binocular microscope. A magnification of 30X was used for the initial determinations of the arthropods. A grid of 5mm squares, etched on the bottom of the dish, facilitated counting. For the oribatid mites, a code designation was assigned to each recognizable form.

We intended to sample primarily the litter stratum; nevertheless, mineral soil was included in each sample. Arthropods resident in the litter-soil interface are probably members of the litter community and could not be collected without including some soil. The depth of soil in a sample was usually less than 1 cm. In the majority of cases the litter was 2 to 3 cm thick.

Each sample was weighed before the arthropods were extracted, and reweighed after removal from the funnel. No relationship appeared between the numbers of oribatids recovered and the "dry" weights of the samples, but any such relationship could have been obscured by the variable amounts of mineral soil present in the samples.

Weekly maximum and minimum temperatures were taken 2 in. above the litter surface in the 3 areas. No striking differences were found between the areas as regards these temperatures (see Figure 1).

Results

From 215 samples of pine forest litter, a total of 30,371 arthropods was obtained. Although 216 samples were brought in from the field, one was discarded because the berlesate was excessively contaminated with soil and could not be examined accurately. Mites were the most abundant arthropods, comprising 82.9% of the total count. Insects constituted 15.8% of the arthropods. This percentage was accounted for primarily by the collembolans, which made up 77.4% of the insects collected. Table I gives the numbers of individuals for the major taxonomic categories collected in the 3 areas together with their combined totals.

Since oribated mites were our primary concern, a complete analysis of the other arthropods will not be given. Many were not separated into species and determinations were obtained for only a small number of the total populations. Nevertheless, the incomplete species list in the appendix does give an indication of the diversity of the

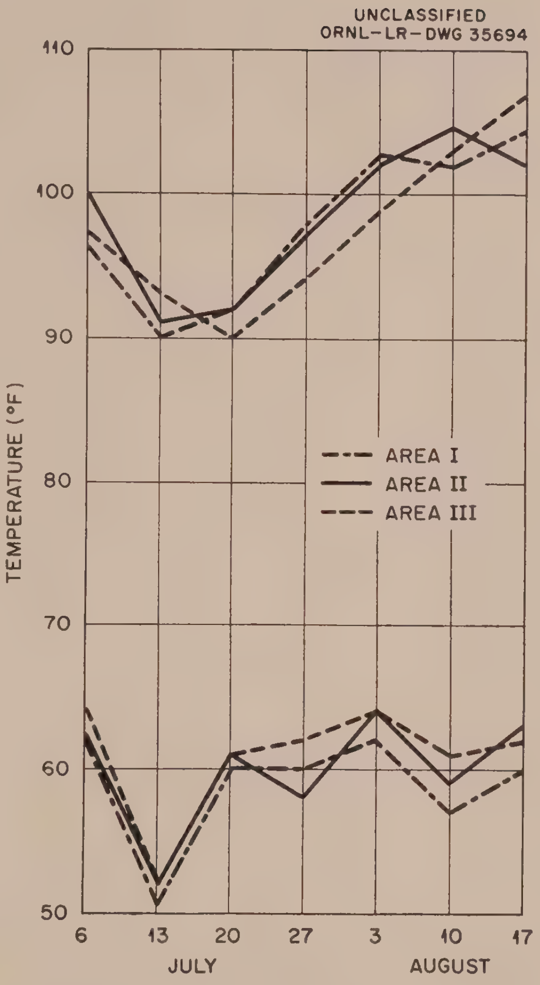

Fig. 1. Weekly maximum and minimum temperatures in Areas I-III.

TABLE I. Number of arthropods obtained from the 3 areas from 215 samples

Anthropod Group	Area I	Area II	Area III	Total all areas
ARACHNIDA				
Pseudoscorpionida	13	28	20	61
Araneida	59	77	25	161
Acarina	7,466	7,964	9,746	25,176
Mesostigmata	274	178	218	670
Trombidiformes	1,810	1,669	2,614	6,093
Sarcoptiformes	5,382	6,117	6,914	18,413
PAUROPODA	12	23	20	55
DIPLOPODA	3	3	2	8
CHILOPODA	10	3	10	23
SYMPHYLA	7	58	15	80
INSECTA	1,630	2,057	1,120	4,807
Protura	75	90	114	279
Thysanura	0	0	1	1
Entotrophi (Japygidae)	16	4	2	22
Collembola	1,334	1,665	721	3,720
Poduridae	44	47	45	136
Onychiuridae	329	524	84	937
Isotomidae	135	271	311	717
Entomobryidae	657	644	203	1,504
Sminthuridae	169	179	78	426
Orthoptera (Blattidae)	0	2	0	2
Isoptera	0	0	38*	38
Corrodentia	6	1	5	12
Thysanoptera	52	43	38	133
Hemiptera	0	2	1	3
adults	0	1	1	
nymphs	0	1	0	
Homoptera	10	22	39	71
adults	6	8	16	
nymphs	4	14	23	
Lepidoptera (larvae)	2	2	3	7
Diptera	47	48	37	132
adults	12	21	20	
larvae	35	27	14	
pupae	0	0	3	
Coleoptera	52	58	45	155
adults	22	33	23	
larvae	30	25	22	
Hymenoptera	36	120	76	232
wasps	24	51	50	
Formicidae	12	69	26	
Total	9,200	10,213	10,958	30,371
Number of samples	72	72	71	215

* 37 termites in one sample.

fauna. A generalized account of the results for these arthropods is given in the following section.

The Arthropod Groups

Collembola

These insects far outnumbered the total for all other insects, as noted above. They were not identified beyond family; Table I gives the total for each family. Members of the family Entomobryidae were the most numerous, and made up 41% of the collembolans. They were followed in rank by the families Onychiuridae (25%), Isotomidae (19%), Sminthuridae (11%), and the least abundant, the Poduridae, which comprised but 4% of the 3720 collembolans collected.

Protura

Second in abundance among the insect orders was the Protura, which represented 5.8% of the insects extracted. The species were not identified.

Hymenoptera

The order Hymenoptera, which ranked 3rd in numbers of individuals, included 107 ants (46% of the Hymenoptera) representing 12 species. Ants occurred in only 46 of the 215 samples, and only 5 of the samples had more than 3 specimens. The largest number in any one sample was 21, all the same species, which suggests a sample from a nest area. This large number of species, considering the small size of the area sampled and the size and energetic behavior of ants, certainly suggests a very heterogeneous ant fauna in the pine forest floor. The remainder of the Hymenoptera were small parasitic wasps.

Coleoptera

Fifty % of the Coleoptera, which was the 4th order in abundance, were adults distributed among 15 families and comprising 35 species. Thirty-five % of the beetles were members of the family Staphylinidae, which was represented by 15 species. Large numbers of rove beetles in the litter are not unusual; others (Pearse 1946, Bohnsack 1954, van der Drift 1950) have reported similar large numbers of these beetles in the litter and surface soil.

Thysanoptera

Thrips occurred in 76 of the 215 samples and were the 5th most abundant insect order. Eight species were determined. The immatures made up 49.6% of the total.

Diptera

Immature Diptera (76 larvae and 3 pupae) which were not identified accounted for 58.9% of this order. Sixteen species of adult flies were recognized in the collections.

Homoptera

The Homoptera, plant sap feeders, occurred in 52 of the samples and most were nymphs (57.7%). Fourteen of the 30 adults were members of the family Cicadellidae and 2 of the adults were coccids.

Pauropoda

Three species of Pauropoda occurred in the samples. Two of the species were described as new (Remy 1957).

Symphyla

The Symphyla which occurred in 46 samples were most abundant in Area II; the largest number obtained from any one sample was 10. They were notably uncommon in Area I where only 4 of the 72 samples had any of these organisms.

Araneida

Of the 161 spiders recovered, 106 were young or adult specimens of a single species, *Lathys immaculata* Chamberlin and Ivie; 93 of these were immatures. *Lathys maculina* Gertsch occurred next most frequently with 11 representatives. In addition to these 2 species, 11 other species were recognized, 6 were determined to species and 5 others to genus. This restricted species composition is in striking contrast to the 61 genera reported by Bohnsack (1954) for the forest floor in an oak-hickory woods; however, he examined a greater surface area, 18 square feet, in contrast to the 3000 sq cm (slightly more than 3 sq ft) which is the basis for this investigation.

Pseudoscorpionida

All but 3 of the 61 pseudoscorpions collected were young individuals, and represented 4 genera. The numbers of individuals were about equally divided between 2 species, *Microbisium confusum* Hoff and *Apochthonius moestus* (Banks). There was one male of the genus *Tyrannochthonius*, and a tritonymph apparently of the genus *Dinocheirus*.

Acarina

The mites (Acarina) composed 82.9% of all the arthropods collected. An average sample had 117 mites. The suborder Sarcoptiformes, which includes the oribatid mites, made up 73.1% of the total; the Mesostigmata comprised but 2.7% and the Trombidiformes 24.2% of the mites.

THE ORIBATID MITES

In all, 6589 adult oribatids representing at least 60 species were collected. It was difficult to make a distinction between the immature mites of the Oribatei and the adult and immature Acaridiae under the 30X magnification; therefore, they were lumped together. The adult oribated mites comprised 35.6% of the Sarcoptiformes. Table II presents the identifications for the oribatid species, the number of adults of each species collected, the number of samples in which the species occurred, and the code designations assigned to the species in the preliminary identifications. Inclusion of the preliminary identifications is necessary because of 2 sorts of errors which were detected in the preliminary identifications. In 2

TABLE II. Species of oribatid mites from pine litter

Code designation	Species identification	Number of individuals collected (6589 total)	Frequency in samples (215 total)
Family Epilohmanniidae			
Epi. I	*Epilohmannia cylindrica* (Berlese)	48	25
Family Nanhermanniidae			
Nan. I	*Nanhermannia areolata* Strenzke	1	1
Nan. II	*Nanhermannia elegantula* Berlese	7	5
Family Lohmanniidae			
	Lohmannia sp.	6	5
Family Hypochthoniidae			
H. I	*Eniochthonius* sp.	3	1
H. II	*Hypochthonius rufulus* Koch	2	1
H. III	*Trhypochthonius americanus* (Ewing)	205	95
Family Camisiidae			
Cam. I	*Nothrus sylvestris* Nicolet	11	7
Cam. II	*Nothrus quadripilus* Ewing	47	24
Cam. III	*Camisia spinifer* (Koch)	11	10
Cam. IV	*Platynothrus peltifer* (Koch)	7	6
Cam. V	*Camisia biverrucata* (Koch)	3	3
Family Belbidae			
Bel. I	*Belba jacoti* (Wilson)	40	33
Bel. II	*Gymnodamaeus* sp.	99	45
Bel. III	*Gymnodamaeus* sp.	3	2
Bel. IV	*Belba nivalis* (Kulcz)	3	2
Bel. V	*Belba* sp. nov.	96	37
Family Eremaeidae			
Er. I	*Ceratoppia bipilis* (Hermann)	43	37
Er. II	*Veloppia* sp.	11	8
Er. III	*Eremobelba* sp.	6	4
Er. IV	*Gen. nov.* near *Ceratoppia*, sp. nov.	3	2
Er. VA	Gen.? sp.?	(mixed)	(mixed)
Er. VB	*Oppia* sp.	(mixed)	(mixed)
Er. VI	*Ceratoppia microseta* Hammer	9	8
Er. VII	*Oppia translamellata* Willmann	2725	197
Er. VIII	*Suctobelba palustris* Forsslund	179	85
Er. IXA	*Suctobelba* sp.	(mixed)	(mixed)
Er. IXB	*Suctobelba* sp.	(mixed)	(mixed)
Er. X	*Oppia subpectinata* (Oudemans)	9	4
Family Carabodidae			
C. I	*Tectocepheus velatus* (Mich.)	82	48
C. II	*Tectocepheus velatus* (Mich.)	356	104
C. III	*Carabodes* sp.	26	6
C. IV	*Carabodes* sp.	7	5
C. V	*Carabodes areolatus*?	2	2
C. VI	*Carabodes areolatus* Berlese	38	8
Family Hermanniellidae			
Herm. I	*Hermanniella robusta* Ewing	2	1
Family Liacaridae			
Lia. I	*Liacarus aequidentatus* Ewing	4	3
Lia. II	*Cultroribula juncta* (Mich.)	530	123
Family Oribatulidae			
Orb. I	*Scheloribates* sp.	208	90
Orb. II	*Liebstadia humeralis*	1	1
Orb. III	*Protoribates lobotrichus* Berlese	95	58
Orb. IV	*Epioribatula* sp.	28	26
Orb. V	*Zygoribatula* sp.	138	43
Orb. VI	*Oribatula* sp.	(mixed)	(mixed)
Family Zetorchestidae			
Z. I	*Zetorchestes equestris* Berlese	48	32
Family Ceratozetidae			
Cer. I	*Ceratozetes* sp.	101	64
Cer. II	*Chamobates* sp.	27	22
Cer. III	*Ceratozetes* sp.	6	6
Cer. IV	*Ceratozetes* sp.	8	4
Family Oribatellidae			
Or. I	*Anachipteria australis*	15	13
Family Microzetidae			
M. I	*Microzetes appalachicola* Jacot	14	10
Family Haplozetidae			
Hap. I	*Rostrozetes* sp. nov.	36	19
Hap. II	*Peloribates* sp.	188	84
Family Pelopidae			
Pel. I	*Parapelops bifurcatus* Ewing	62	20

(Table II. Continued)

Code designation	Species identification	Number of individuals collected (6589 total)	Frequency in samples (215 total)
Pel. II	*Pelops* sp.	77	32
Pel. III	*Pelops* sp.	(mixed)	(mixed)
Family Galumnidae			
Gal. I	*Galumna* sp.	35	23
Gal. II	*Galumna* sp.	257	113
Gal. III	*Galumna virginiensis* Jacot	12	10
Family Parakalumnidae			
Park. I	*Parakalumna robustum*? Jacot	3	2
Park. II	*Parakalumna* sp.	1	1
Family Phthiracaridae			
P. I	*Pseudotritia loricata* (Rathke)	92	52
P. II	*Steganacarus terrapenae* Jacot	15	12

cases, different preliminary forms were identified as belonging to the same species. These forms have been kept separate in Table II, since they are separable under the wide-field microscope on characters not apparent on mounted specimens. It seems likely, however, that the forms in these cases are conspecific. In 3 cases, the preliminary form was found to consist of 2 species. Since the counts for these species cannot be corrected, the species must be deleted from considerations of relative abundance. In Table II these species are designated as "mixed."

Relative Abundance of Species

The abundances of the oribatid species, as given in Table II, show a wide range. *Oppia translamellata* Willmann, a small mite measuring about 240 microns in length, is clearly the most abundant species. It was represented by 2725 individuals and was found in 197 samples. Many of the species, however, were represented by few individuals. The relative abundance of the more numerous species is shown in Table III, which lists these species in order of descending abundance, and gives the number of individuals, the percentages of the total individuals, and the cumulative percentages of the total. The 9 species listed include more than 70% of the individuals collected.

Table III. Numbers collected of the more abundant oribatid species (adults) in 215 samples of litter

Species	Number of specimens	Per cent of total	Cumulative per cent of total
Oppia translamellata	2725	41.2	41.2
Cultroribula juncta	530	8.0	49.2
Tectocepheus velatus	356	5.4	54.6
Galumna sp.	244	3.7	58.3
Scheloribates sp.	208	3.2	61.5
Trhypochthonius americanus	205	3.1	64.6
Peloribates sp.	179	2.7	67.3
Suctobelba palustris	176	2.7	70.0
Zygoribatula sp.	138	2.1	72.1
Remaining 51 species	1828	27.9	100.0
Totals	6589	100.0	

Evidently, there is a continuous distribution of the abundance of individuals for the various species. Similarly, the frequency distribution for the occurrence of species in samples appears to be continuous. Figure 2 shows the occurrence of the oribatid species in intervals of 10 samples; thus, 28 species occurred in 1-10 of the samples, 4 species occurred in 11-20 of the samples, and so on. The shape of the resulting curve is somewhat dependent upon the size of the class used for illustration, but in any case the curve shows an exponential decrease. Considerations of abundance and frequency provide no criteria for separating the species into such categories as "abundant," "common," or "rare." Nevertheless, for purposes of analysis and discussion, some distinction must be made between the more numerous and less numerous species. We have selected, arbitrarily, the 9 most abundant and most frequent species for further discussion. These species are the ones listed in Table III.

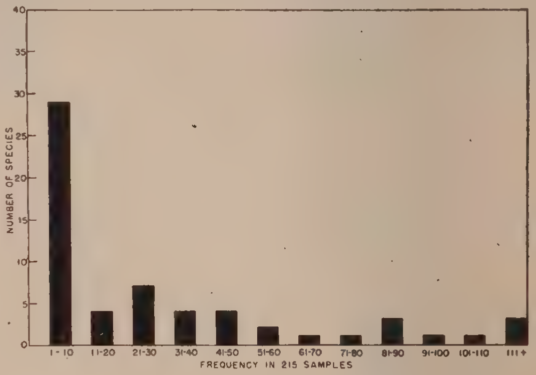

Fig. 2. Frequency of occurrence of the species of adult oribatid mites in the 215 samples of litter.

Distribution of Individuals in Samples

For each of the more abundant species, it was necessary to examine the distribution of the number of individuals per sample. Each frequency distribution was then compared with a Poisson distribution of the same mean, in order to determine whether the animals were distributed at random. In each case the distribution of individuals per sample showed "clumping." Figure 3 illustrates the distribution of individuals per sample for *Cultroribula juncta* (Mich.), in comparison with a Poisson distribution of the same mean. The excess of absences and of large samples clearly indicates aggregation or lack of homogeneity. Such distributions are commonly found in samples of arthropods (Cole 1946). While it is possible to explain the aggregations for some arthropods (for example, ants) on a social basis, so little is known of the habits of oribatid mites that few conjectures can be made. Despite the apparent uniformity of the forest floor, some patchiness must exist. Similar results were obtained by Salt and Hollick (1946) in a study of the distribution of wireworms in a seemingly uniform grassland.

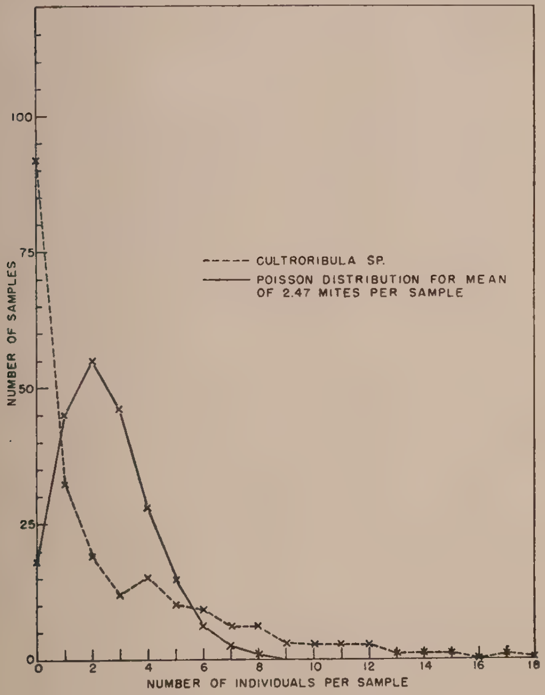

FIG. 3. Frequency distribution of numbers of adult *Cultroribula juncta* in samples, as compared to a Poisson distribution of the same mean.

Local Variation in Numbers

For the more abundant species, variation in numbers was examined by means of an analysis of variance. It was necessary to transform the data; a square-root transformation ($\sqrt{x + 0.5}$) was found to be satisfactory. The analysis is illustrated in Table IV, and the data for *Cultroribula juncta* (Mich.) are given as an example. Since the arrangement was in part hierarchic (stations in areas) and in part orthogonal (weeks) the tests of variance ratios were not straightforward. In general, the main effects were tested over the appropriate interactions when the latter were significant; when the interactions were not significant, the station and area effects were treated as hierarchic. In Table IV, the mean squares are significant (P = 0.01) for stations in areas, weeks, and the stations in areas by weeks interaction. Thus, differences existed between the average numbers of mites per station within each area, and between the average numbers of mites per week; the significant interaction shows that the relationship between means in the stations was not constant through time. In this example, differences between the areas are no greater than the differences between stations within the areas.

TABLE IV. Results of analysis of variance on *Cultroribula juncta* (counts transformed by $\sqrt{x + 0.5}$)

	Sum of squares	Degrees of freedom	Mean square
Areas	22.9294	2	11.4647
Stations in areas	38.5526	6	6.4254[a]
Weeks	20.6939	7	2.9536[a]
Areas by weeks interaction	5.3705	14	0.3836
Stations in areas by weeks interaction	31.0688	42	0.7379[b]
Error	47.0978	143	0.3294
Total	165.7139	214	

[a] Significant at P=0.01 relative to 0.7379.
[b] Significant at P=0.01 relative to 0.3294.

Table V summarizes the results of variance ratio tests for the more abundant species. Seven of the 9 species show significant differences between stations within areas. Significant differences between weeks occur in 6 of the 9 species, in spite of the short duration (8 weeks) of the sampling period. For 4 of the 9 species, significant differences between the areas are shown. Table VI presents the mean number of individuals per sample for each station. Of particular interest are *Tectocepheus velatus* (Mich.), *Scheloribates* sp., *Peloribates* sp., and *Zygoribatula* sp., for which differences between areas are significant. These differences are due to low numbers in one area for *Techtocepheus velatus* (Mich.), *Scheloribates* sp., and *Peloribates* sp. *Zygoribatula* sp. is low in 2 of the 3 areas. Also, differences between stations within areas are evident for many of the species shown in Table VI.

For those species showing significant change with time, the following variations were noted. Peaks of abundance occurred in the middle of the sampling period for *Oppia translamellata* Willm. and *Suctobelba palustris* Forsslund. *Peloribates* sp. increased during the sampling period; *Cultroribula juncta* (Mich.) and *Trhypochthonius amer-*

TABLE V. Summary of results of analysis of variance tests on the more abundant species

Source of variation	Areas	Stations in areas	Weeks	Areas by weeks interaction	Stations in areas by weeks interaction
Oppia translamellata	n.s.	**	**	**	n.s.
Cultroribula juncta	n.s.	**	**	n.s.	**
Tectocepheus velatus	**	**	n.s.	n.s.	n.s.
Galumna sp.	n.s.	**	**	n.s.	n.s.
Scheloribates sp.	**	n.s.	n.s.	*	n.s.
Trhypochthonius americanus	n.s.	**	**	*	n.s.
Peloribates sp.	**	n.s.	*	n.s.	*
Suctobelba palustris	n.s.	**	**	n.s.	n.s.
Zygoribatula sp.	*	**	n.s.	n.s.	n.s.

* Significant at P=0.05.
** Significant at P=0.01.
n.s. Not significant.

icanus (Ewing) increased in 2 of the 3 areas. *Galumna* sp. increased during the first 4 weeks. The total number of oribatids collected tended to increase with time. It should be noted that these increases represent transformation to the adult stage, rather than actual reproduction. While few life histories have been worked out for the oribatids, the evidence indicates that at least 30 days are required to complete the average life history under ideal conditions.

Relations Between Species

Some information on the associations between species may be deduced from a sampling regimen. This may be done by evaluating the occurrences in samples of the species in order to identify recurring groups for the species. Evaluation of the number of joint occurrences in samples for 2 species may be made with a 2 x 2 contingency table (Cole 1949). The trellis diagram methods are more subjective methods for finding the associations between species in samples (Macfadyen 1954). Recently, Fager (1957) published a method for evaluating the significance of the number of joint occurrences of species in samples. Also, a method for the detection of recurrent groups of species, by arrangement in a trellis diagram, was suggested. Fager finds the expected number of joint occurrences (expected J) as:

$$\text{Expected J} = \frac{n_a n_b}{n_a + n_b}$$

where n_a is the number of samples containing species a and n_b is the number of samples containing species b. Probability of joint occurrences is thus related to the number of samples in which either or both species occurred, rather than to the total number of samples taken. A one-tailed t-test is used for positive affinity (negative affinity is considered "potentially subject to too many unavoidable errors"). Minimum values for joint occurrences (J) which are significant at the $P = 0.05$ level are tabulated.

The minimum significant values for J are based on a normal approximation, so that the closer the ratio n_b/n_a approaches 1, the closer the approximation to the true value. Fager suggested an upper limit of 2 for this ratio. Direct application of this interesting method to the present data proved impossible; as can be seen from Table II, *Oppia translamellata* Willm. cannot be compared with most of the others, since only those species with 98 or more occurrences (197/2) could be tested. Even the last of the 9 more abundant species, *Zygoribatula* sp., with 43 occurrences, could not be compared with more than half of the species in the study. To overcome this difficulty, the acceptable maximum for the ratio n_b/n_a was stretched to 2.5; also, the 3 replicate samples taken each week in each station were lumped into one. By these devices it was possible to test the 26 most abundant species against one another for joint occurrences significantly greater than chance.

When the significant joint occurrences had been tabulated, a recurrent group emerged which contained 9 species. This recurrent group differs

TABLE VI. Mean numbers of adult oribatid mites per sample, by stations (abundant species only)

Species	AREA I			AREA II			AREA III		
	Station A	Station B	Station C	Station D	Station E	Station F	Station G	Station H	Station I
Oppia translamellata	5.67	11.42	3.08	14.83	8.25	21.63	6.21	30.13	12.87
Cultroribula juncta	5.79	0.50	0.79	3.17	3.17	5.04	0.50	2.71	0.43
Tectocepheus velatus	0.00	0.04	0.21	4.79	3.71	2.50	1.63	1.08	0.91
Galumna sp.	1.21	1.25	1.17	1.58	2.63	0.33	0.33	1.88	0.35
Scheloribates sp.	1.08	1.96	1.71	1.54	0.92	1.38	0.00	0.04	0.04
Tryhpochtonius americanus	1.83	2.17	0.54	0.75	1.08	0.63	0.42	0.13	1.04
Peloribates sp.	0.00	0.13	0.21	1.79	1.58	1.25	0.58	1.38	0.96
Suctcbelba palustris	0.71	0.38	0.88	0.42	0.54	1.79	0.13	2.21	0.43
Zygoribatula	0.00	0.00	0.00	0.00	0.04	0.04	3.04	0.38	2.35

from the previously noted group of "more abundant" species which had been aribtrarily selected, only in that *Ceratozetes* sp. replaces *Zygoribatula* sp. as the 9th member. The remaining species show affiliation only with members of the recurrent group, except for significant joint occurrences of *Belba jacoti* (Wilson) with *Protoribates lobotrichus* Berl.

These findings tend to corroborate the arbitrary selection of the 9 most abundant species for detailed analysis. Of more interest is the emergence of a single group of species, despite the differences between areas suggested by analysis of variance results. The finding of a single group suggests that a single fauna has been sampled.

Less-Abundant Species

Although the discussion and analyses have been centered around the 9 "more abundant" species, most of the species in the study fall into the category "less abundant." These less abundant species include less than 30% of the individual oribatids collected. Although most of these species are represented by small numbers, some observations on the distribution of these species are pertinent.

Of the 48 species for which counts are available, 12 occurred in one station only. These "restricted" species are of particular interest since their presence in a station might be indicative of environmental factors peculiar to the stations. On the other hand, these species may be so rare as to occur in only one or 2 samples due to chance alone. Extreme rarity would seem to be the case for 7 of the 12 "restricted" species. However, *Oppia subpectinata* (Oud.), restricted to Station A, was represented by 9 individuals in 4 samples. Also in Station A, *Nanhermannia elegantula* Berl. occurred in 5 samples (7 individuals). *Eremobelba* sp. in Station B, *Platynothrus peltifer* (Koch) in Station C, and *Ceratozetes* sp. in Station H, occurred in several samples in the respective stations. It seems likely that these 5 species were truly restricted—or at least more numerous—in the stations in which they were collected. Probably these results for the less abundant species are manifestations of the same sort of between-station variation as was shown quantitatively for the more abundant species.

Of the 36 species which occurred in more than one station, 7 were restricted to one of the areas, 12 to 2 of the areas, and 17 were found in all 3 areas. Only 2 of these species, *Epioribatula* sp. and *Pseudotritia loricata* (Rathke), were found in every station. These distributions, also, seem similar to those shown for the more abundant species.

Discussion

The estimate obtained for the number of arthropods in pine litter is similar to those obtained by other authors for various soil and litter situations. The number of arthropods was estimated at 102,000 per square meter. A quite similar estimate 9,759 arthropods per square foot (105,000 per sq m) for decidious litter and one inch of humus in Pennsylvania was reported by Hoffmann *et al.* (1949). These estimates are considerably greater than those suggested by Pearse (1946) of 1719 per sq ft (18,500 per sq m) of litter and 5 inches of soil based on a year's collection in deciduous and conifer stands in the Duke Forest, North Carolina, or the annual average of 42,750 per sq m of litter reported by Bohnsack (1954) in an oak-hickory forest in southern Michigan. However, all of these estimates greatly exceed the low figure of Allee *et al.* (1949) of 3500 microarthropods per sq m of leaf mold in an oak-elm-maple forest in Illinois. All of the density approximations are strikingly low when compared with the results of Forsslund (1945), who estimated a population of 1,089,000 arthropods per sq m in the surface 4 inches of a spruce-pine-beech forest of Sweden. The estimate concluded from the present study is also considerably less than similar reports by some investigators of nonforested areas. Hairston and Byers (1954) calculated a population of 259,304 arthropods per sq m in the surface 8 inches of an old field in southern Michigan. This figure corresponds very closely to the 263,658 per sq m reported by Salt *et al.* (1948). Quantitative comparisons of this nature do not afford alone an adequate index of the arthropods of a particular fauna, but they do emphasize the magnitude of variation in estimates obtained by different workers, particularly investigators concerned with the forest floor populations. Probably, dissimilarities in the methods of collecting the arthropods—number, location, size, and depth of the samples, month of sampling, procedures employed in the removal of the arthropods—all materially contribute to the variations reported. Forsslund (1948) by direct examination of small samples increased his earlier estimate to 2,300,000 arthropods per square meter, which represents a twofold increase over his previous phenomenal figure. It seems apparent that realistic comparisons of density per unit area cannot be made unless similar procedures are followed.

The Collembola and Acarina are the 2 most ubiquitous and abundant groups of arthropods in the litter, and their contribution to this fauna has been reported as approaching or exceeding 90%. In this investigation they composed 95% of the total arthropods. Dogiel and Efremoff (1925) found the Collembola and Acarina comprising 90% of the arthropods in a spruce forest in Russia. Lunn (1939) stated that the Acarina and Collembola made up 87% of the logmold and 75% of the leaf mold populations. Park and Auerbach (1954) reported these 2 groups comprising 88% of the tree hole populations, and Bohnsack (1954) found them to make up 96% of the litter in an oak-hickory forest.

The results for the oribatid mite data, while more extensive than those for the other arthropods, must still be examined with caution. Since we can deal only with the adult mites, species recorded as low in abundance could conceivably be represented by great numbers of immature stages. The extraction process, also, is likely to have different efficiencies for the different species. These difficulties are encountered in any such study, and are less important in comparisons of areas than in the comparisons of the abundances of species.

Comparison of the list of oribatid species collected with the lists in such thorough studies as those of Hammer (1944), van der Hammen (1952), and Schweizer (1956) shows that the oribatid fauna of pine litter in the Oak Ridge area is an extensive one. Although the present study was based upon samples from rather limited areas, the list of species reveals a broad representation of oribatid families. Doubtless further collecting will reveal species not included in the list. Some of the species are evidently quite widely distributed; for example, *Nanhermannia elegantula* Berl, *Hypochthonius rufulus* Koch, *Camisia spinifer* (Koch), *Ceratoppia bipilis* (Hermann), *Tectocepheus velatus* (Mich.), and *Carabodes areolatus* Berl. are species which occur frequently in faunal lists from other areas. Discussion of the distributions of the species is beyond the scope of this work; it was our aim to examine variability on a much smaller geographic scale.

The results of the analysis of variance tests (Table V) on the abundant oribatid species clearly show the wide local variability of the species. All 9 of these species differ significantly either between areas or between stations within areas, and 2 species show variation at both levels. In view of this variation, it is difficult to give a simple characterization of the oribatid fauna of pine litter. *Oppia translamellata* Willm. was the most abundant species in the study; however, in Station A it was exceeded in numbers by *Cultroribula juncta* (Mich.) (Table VI). Likewise, the latter species, which was 2nd in abundance in the study as a whole, was not 2nd in any except stations F and H. The 3 study areas themselves can be readily characterized by the abundances of the 4 species which showed significant differences between areas; namely, *Tectocepheus velatus* (Mich.), *Scheloribates* sp., *Peloribates* sp., and *Zygoribatula* sp. Area I had a (comparative) abundance of *Scheloribates* but was deficient in numbers of the other 3 species; Area II was deficient in numbers of *Zygoribatula* sp. but not in numbers of the other 3 species; and Area III was deficient in numbers of *Scheloribates* but had an abundance of *Zygoribatula* sp. (Table VI). Examination of Table VI indicates that these differences between areas were not minute ones, but involved rather large differences in relative abundance. Certainly it would be possible to characterize in a similar way the stations within each area, and probably the entire group of 9 stations could be so characterized. Thus, significant variations occur at each level of the hierarchic sampling scheme.

One statistical implication of this analysis is that experimentation on litter decay should be made on relatively small blocks in order to minimize the variability introduced by initial differences between experimental plots. On the other hand, a sampling scheme which seeks to characterize the fauna of a given type of vegetation should include enough different areas and stations of this community so that variations on all levels will be included.

The results of the trellis diagram method, as noted, suggest that the species studied belong to a single fauna, despite the differences between areas in abundances of certain species. If this were not the case, the trellis diagram method should have shown more than one recurrent group of species; however, all of the abundant species showed association with one another (with the exception of *Zygoribatula* sp.). It seems reasonable that the variety of factors, physical and biological, by which the stations and areas undoubtedly differ produces a patchwork of environmental conditions, and that the different abundances of the species result from their responses to these factors. Somewhat similar conclusions were reached by Hairston and Byers (1954) in a study of the soil arthropods of an abandoned field in southern Michigan, where the occurrence of aberrant samples was found to be related to locations near the edge of the field or to trees. In the present work, no such explanations can be offered, but it is concluded that local variations in the habitat have been sampled, despite the uniform appearance of the forest floor.

SUMMARY

From 215 samples (approximately 3000 sq cm) of pine forest litter taken in the Oak Ridge area during the summer of 1956, a total of 30,371 arthropods were obtained. Of this number, mites (Acarina) comprised 82.9%, collembolans 12.2%, and other insects 3.6%. Particular attention was directed toward the oribatid mites.

The samples were taken from 3 similar areas, each of which was represented by 3 stations. Three samples were taken from each station each week for a period of 8 weeks during July and August. Thus, a hierarchic measure of the variation in abundance was obtained for the more abundant oribatid species. Results of analysis of variance tests showed that significant variation occurs both between stations within areas and between the areas, for certain of the abundant oribatid mites. Fager's (1957) trellis diagram method was used to detect significant joint occurrences between species; only a single recurrent group of species was found.

Although the 3 study areas have different relative abundances of certain of the more numerous species, it is concluded that the differences between areas represent local variations in a single oribatid fauna, rather than elements of 2 or more faunas.

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APPENDIX

List of arthropods collected from the litter of pine forests on the AEC Controlled Area, Oak Ridge National Laboratory. The tabulation includes only those arthropods (except Oribatei) for which determinations by specialists were obtained. Notably absent from the list are the mites and collembolans.

ARACHNIDA

PSEUDOSCORPIONIDA
- *Apochthonius moestus* (Banks)
- *Dinocheirus* sp.
- *Neobisium* (?)
- *Microbisium confusum* Hoff
- *Tyrannochthonius* n. sp. (?)

ARANEIDA
- Agelenidae
  - *Cirurina* sp.
- Clubionidae
  - *Phrurotimpus* sp.
- Dictynidae
  - *Lathys immaculata* Chamberlin & Ivie
  - *Lathys maculina* Gertsch

- Gnaphosidae
  - *Drassyllus* sp.
  - *Gnaphosa sericata* Koch
- Linyphiidae
  - *Ceraticelus* sp.
  - *Eperigone tridentata* Emerton
  - *Erigone autumnalis* Emerton
- Lycosidae
  - *Pardosa* sp.
- Salticidae
  - *Phidippus clarus* Keyserling
  - *Neonella vinnula* Gertsch
- Theridiidae
  - *Steatoda americana* Emerton

PAUROPODA

PAUROPIDAE

- *Allopauropus (Decapauropus) bohnsacki* Remy
- *Pauropus dukensis* Starling (may be in family Scleropauropidal Remy, 1957)
- *Stylopauropus (Donselotauropus) quadrisulcus* Remy

INSECTA

THYSANOPTERA

- (Suborder Terebrantia)
- Thripidae
  - *Frankliniella tritici* (Fitch)
  - *Sericothrips annulipes* Hood
  - *Sericothrips* sp. (*apicalis?*)
- (Suborder Tubulifera)
- Phlaeothripidae
  - *Eurythrips watsoni* Hood
  - *Hoplothrips angusticeps* (Hood)
  - *Lissothrips muscorum* Hood
- Urothripidae
  - *Trachythrips watsoni* Hood

DIPTERA (adults)

- Psychodidae
  - *Telmatoscopus* sp.
  - *Psychoda alternata* Say
- Tendipedidae (Chironomidae)
  - *Cricotopus* sp.
- Heleidae (Ceratopogonidae)
  - *Culicoides* sp.
  - *Lasiohelea* sp.
- Lycoriidae (Sciaridae)
  - *Bradysia* sp.
  - *Pnyxia* sp.
- Itonididae (Cecidomyiidae)
  - *Anarete* sp.
  - *Itonida* sp.
  - *Lestodiplosis* sp.
  - *Mycodiplosis* sp.
- Empididae
  - *Drapetis* sp.
- Milichiidae
  - *Leptometopa latipes* (Mg).
- Phoridae
  - *Megaselia* sp.
- Sphaeroceridae (Borboridae)
  - *Leptocera* sp.

COLEOPTERA (adults)

- Carabidae
  - *Bembidion* sp.
  - *Tachys laevus* (Say)
- Staphylinidae
  - (Subfamily Paederinae)
  - *Astenus discopunctatus* Say
  - *Astenus prolixus* Er.
  - *Echiaster (Leptogenius) brevicornis* Csy.
  - *Palaminus* sp.
  - *Scopaeus* sp.
  - (Subfamily Staphylininae)
  - *Diochus nanus* Er.
  - *Philonthus hepaticus* Er.
  - *Philonthus* nr. *umbratilis* Grav.
  - (Subfamily Tachyporinae)
  - *Mycetoporus flaviocollis* LeC.
  - (Subfamily Oxytelinae)
  - *Carpelimus* sp.
  - *Oxytalus exiguus* Er.
  - (Subfamily Aleocharinae)
  - *Atheta* sp. I
  - *Atheta* sp. II
  - *Oxypoda* sp.
  - (Subfamily Euaesthetinae)
  - *Edaphus nitidus LeC.*
- Cantharidae
  - *Malthodes concavus* Lec.
- Mordellidae
  - *Mordellistena* perhaps *infima* Lec.
- Anthicidae
  - *Anthicus cervinus* Laf.
  - *Anthicus floralis* (L.)
- Throscidae
  - *Throscus chevrolati* Bonv.
- Monotomidae
  - *Monotoma fulvipes* Melsh.
- Cucujidae
  - *Ahasversus advena* Walti.
  - *Laemophloeus biguttatus* Say
- Crytophagidae
  - *Tomarus pulchellus* Lec.
- Mycetophagidae
  - *Typhaea sterocorea* L.
- Lathridiidae
  - *Coninomus australicus* Bel.
  - *Corticaria elongata* Gyll.
  - *Melanophthalma distinguenda* (?) Com.
  - *Melanophthalma simplex* Lec.
- Tenebrionidae
  - *Anaedus brunneus* (Ziegl.)
- Anobiidae
  - *Catorama* sp.
- Scarabaeidae.
  - *Ataenius schwartzi* Linell
- Chrysomelidae
  - *Epitrix hirtipennis* (Melsh.)

HYMENOPTERA

- Formicidae
  - *Amblyopone pallipes* (Haldeman)
  - *Aphaenogaster rudis* Emery
  - *Brachymyrmex depilis* Emery
  - *Leptothorax curvispinosus* Mayr
  - *Monomorium minimum* (Buckley)
  - *Myrmecina americana* Emery
  - *Myrmica pinetorum* Wheeler
  - *Paratrechina melanderi* (Wheeler)
  - *Pheidole dentata* Mayr
  - *Ponera coarctata pennsylvanica* Buckley
  - *Solenopsis molesto* (Say)
  - *Tapinoma sessile* (Say).

SOME OBSERVATIONS ON THE FOOD COACTIONS OF THE COMMON BOX TURTLE, *TERRAPENE C. CAROLINA*

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Previous observations on the foods utilized by the common box turtle, *Terrapene c. carolina* Linnaeus (Schmidt 1953), indicate an omnivorous diet. Cahn (1937) suggests that more plant than animal matter is eaten while Allard (1935) reports that animal food is preferred. Apparently the diet is quite varied, as several authors (Conant 1938, Moore 1943, Pope 1947, Allard 1948, Smith 1950 and Creaser 1940) state that fruit and other plant parts are important, emphasizing also the value of mushrooms, insects, earthworms, crayfishes, gastropods, myriapods, fishes, frogs, and carrion.

An attempt has been made to evaluate the quantitative aspects of foods taken by the common box turtle and to appraise this utilization in the light of food items available to this reptile. Examination of the contents of the digestive tracts of 117 specimens from west central southern Illinois, and an analysis of available animal foods in one woodland habitat, have provided the data for this publication.

All turtles utilized were taken in the vicinity of Carbondale, Illinois. This region of southern Illinois is considered an agricultural area with approximately 55% in active agricultural use, 15% idle, and 30% forested (King and Winters 1952, Ross and Case 1956). The natural vegetative types tend to reflect the intermingling of prairie and forest plants which originally characterized the glaciated portion of southern Illinois. Except for the sites of various waterways, the land features upland characteristics which are poorly drained because of an immature topography and an impervious subsoil (Wascher *et al.* 1950). Average rainfall approximates 40-44 inches and average temperatures provide a growing season of about 200 days (Page 1949). As a result of the latitude the fauna is rich being represented by species of both northern and southern affinities.

Methods and Materials

Box turtles available for study were collected during routine field investigations, March to October of 1955 and 1956 (Table I). Many (74) of the specimens were collected from a bobwhite quail research area which was visited almost daily during the period of this study.

Table I. The yearly and monthly distribution of the captures of common box turtles

	March	April	May	June	July	August	September	October	Totals
1955..	1	—	22	11	9	2	2	11	58
1956..	—	1	11	1	11	22	6	7	59
Totals.	1	1	33	12	20	24	8	18	117

Shortly after collecting the turtles the digestive tracts were removed, slit lengthwise, the contents flushed into a fine sieve, and then preserved in 10% formalin until examined. The approximate volumes of the entire contents of several digestive tracts were measured by water displacement, the same technic employed to determine volumes of individual food items.

For identification, the contents of the digestive tracts were examined with the aid of a dissecting microscope. Because the food items often were disintegrated and usually only partially present, identification was difficult. It was necessary to base most of the determinations on the structure of durable parts.

Numerous general keys including Comstock (1947), Essig (1947), Chu (1949), Edwards (1949), and Borror and Delong (1954) were employed for the identification of insects; for selected groups Forbes (1922), Graham (1922), Curran (1934), Kellog (1894), and Peterson (1951a and 1951b) were consulted. A reference collection of insects collected locally was invaluable.

Reliance for identification of Gastropoda was placed on structural features of the mouthparts as determined from local species of snails and slugs and descriptions in the literature (Binney 1875, Baker 1902, and Pilsbry 1939, 1940, 1946, 1948). The identification of most gastropods is believed to be reasonably accurate; however, radulae from *Polygyra leporina, Mesodon appressus, M. pennsylvanicus, Tridopsis albolabris* and *Succinia concordialis* are not identified with absolute certainty because local representatives of these forms were not examined.

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[1] This study represents a contribution from Project No. 44, Cooperative Wildlife Research Laboratory, Southern Illinois University. Appreciation is expressed to the several members of the Laboratory who assisted the study.

The isopods, which consisted almost entirely of *Armadillidium vulgare,* were identified according to Van Name (1936) and Hatchett (1947). The structure of scales was the basis for identification of most reptilian food items; comparison was made with specimens collected locally. The distinction between *Thamnophis sauritus* and *Storeria occipitomaculatus* and between the several species of *Natrix* could not be established by scale characteristics. Birds, represented only by a few feathers, were identified by use of a reference collection and Chandler (1916). Determinations of mammalian food items were based on guard hairs; their absence in several digestive tracts, however, prevented complete identification of some items. Valuable aids were Hausman (1930), Mathiak (1938), Mayer (1952), and reference slides prepared from hair of mammals collected locally Fishes were identified from scales (Lagler 1952 and Cockerell 1911) using a series of reference slides from local species. The determination of amphibian food items, based on intact specimens, was according to Cagle (1941). Seeds were identified by comparison with an extensive local collection. A detailed classification of Diplopoda, Chilopoda, Arachnida, Annelida and Decapoda was not attempted.

In an effort to relate availability of food items to their utilization by this animal during July, August, and September of 1956, the fauna of 8 square meters of duff from a woodlot and that of logs were analyzed. The animal contents of the digestive tracts of 15 terrapins, collected during the same period, were compared to the forms recorded in the duff and logs. The presence of some animals in the diet and their absence in the sampled environment suggested that sampling was inadequate.

Discussion

The volume of food taken from the individual digestive tracts ranged from 65.0 to 0.5 cubic centimeters and was divided arbitrarily into 3 volumetric groups: 25.0 to 65.0, 15.0 to 25.0, and 0.5 to 15.0 cc. A comparison of values obtained for May through October indicated that the consumption of food increased in spring until June

Table II. Monthly percentages of 3 volume classes of food recorded in digestive tracts of the common box turtle, Carbondale, Illinois

Volume Classes	May	June	July	August	September	October
25.0-65.0 cc.	15	50	20	13	13	0
15.0-25.0 cc.	58	42	55	46	25	22
0.5-15.0 cc.	27	8	25	41	69	78

Table III. Major food groups with representative food items which occurred in digestive tracts of the common box turtle, *Terrapene c. carolina* southern Illinois, 1955-1956

Food Items	Percentage* Frequency of Occurrence	Average Frequency	% Volume
PLANT	89	—	51.6
Undetermined	87	—	34.2
Determined (Seeds)	74	14.30	17.4
Gramineae	37	—	—
Undetermined	25	—	—
Bromus	12	—	—
Paspalum	3	—	—
Hordeum	3	—	—
Rosaceae	29	—	—
Rubus	21	—	—
Prunus	5	—	—
Ebenaceae-*Diospryos*	7	—	—
Moraceae-*Morus*	5	—	—
Polygonaceae-*Polygonum*	5	—	—
Caryophyllaceae	4	—	—
Compositae	4	—	—
Ambrosia	3	—	—
Chenopodiaceae	4	—	—
Rubiaceae	4	—	—
Galium	3	—	—
Cyperaceae	3	—	—
Vitaceae-*Vitis*	3	—	—
Leguminosae	3	—	—
ANIMAL	98	—	46.3
Undetermined	15	—	2.3
Determined	93	24.90	44.0
Insecta	92	23.40	19.6
Undetermined	31	—	—
Coleoptera	73	—	—
Undetermined	45	—	—
Scarabaeidae	35	—	—
Phyllophaga	17	—	—
Cotinis	4	—	—
Canthon	4	—	—
Aphodiinae	4	—	—
Carabidae	34	—	—
Curculionidae	6	—	—
Lampyridae	4	—	—
Staphylinidae	4	—	—
Nitidulidae	3	—	—
Chrysomelidae	3	—	—
Lepidoptera	51	—	
Undetermined	34	—	—
Phalonidae	10	—	—
Hymenoptera	51	—	—
Undetermined	9	—	—
Formicidae	50	—	—
Chalicididae	3	—	—
Diptera	36	—	—
Orthoptera	21	—	—
Undetermined	3	—	—
Locustidae	10	—	—
Gryllidae	8	—	—
Hemiptera	9	—	—
Collembola	7	—	—
Homoptera	4	—	—
Gastropoda	72	6.10	10.6
Undetermined	15	—	—
Polygyridae	32	—	—
Undetermined	20	—	—
Triodopsis albolabris	7	—	—
Polygyra leporina	7	—	—
Mesodon thyroidus	5	—	—
M. appressus	3	—	—
M. inflectus	3	—	—
T. tridentata	3	—	—
Limacidae	24	—	—
Undetermined	10	—	—
Deroceras laeve	20	—	—
D. reticulatum	9	—	-

(Table III. Continued)

Food Items	Percentage* Frequency of Occurrence	Average Frequency	% Volume
Succineidae	21	—	—
Undetermined	3	—	—
Succinea avara	19	—	-
Zonitidae	17	—	—
Undetermined	2	—	—
Mesomphix cupreus	10	—	—
Ventridens	6	—	—
Zonitoides	3	—	—
Philomycidae-*Pallifera dorsalis*	5	—	—
Endodontidae	4	—	—
Helicodiscus parallelus	3	—	—
Pupillidae	3	—	—
Isopoda	14	0.50	3.5
Undetermined	7	—	—
Armadillidium vulgare	6	—	—
Diplopoda	47	0.90	2.5
Mammalia	44	0.85	1.6
Undetermined	15	—	—
Rodentia	10	—	—
Cricetidae	8	—	—
Microtus	7	—	—
Lagomorpha-*Sylvilagus*	9	—	—
Insectivora	9	—	—
Decapoda	9	0.10	1.5
Reptilia	6	0.10	1.3
Aves	20	0.20	1.3
Undetermined	11	—	—
Passeriformes	8	—	—
Annelida	5	0.10	1.0
Amphibia	1	0.01	0.4
Arachnida	21	0.50	0.3
Acarina	17	—	—
Araneae	7	—	-
Chilopoda	6	0.10	0.2
Pisces	4	0.04	0.2
Centrachidae	3	—	—
UNDETERMINED	15	—	2.1

* Items occurring in less than a 3% frequency not included.

at which time 50% of the digestive tracts yielded 25.0 to 65.0 cc of food (Table II). The volume of food decreased after June through October when 78% of the terrapins contained less than 15.0 cc. These data suggest that food consumption was possibly related to weather factors and/or breeding activities as well as availability of acceptable food.

General Food Habits

Although some of the items such as mites probably were ingested accidentally, the majority are presumed to have been taken as food. The criteria used to present these data, frequency of occurrence, average frequency and average percentage volume, should be considered together if a correct interpretation is to be placed on the findings; any one criterion would result in less accurate conclusions.

In excess of 130 different kinds of food items were recorded in the diet of the common box turtle (Table III). The more important food groups as indicated by % volume included: unidentified plant material (34.2%), insects (19.6%), seeds (17.4%), gastropods (10.6%), isopods (3.5%) and diplopods (2.5%). According to frequency of occurrence the top-ranking food groups were similar to that suggested by volume, except for the isopods. Contrary to the findings of other authors, the annelids seemed to be of minor importance even though they were frequently seen in the soil immediately below the leaves in woodland areas where many of the terrapins were captured. Virtually all utilization of vertebrates was believed to represent carrion feeding. These were never represented by more than hair and feathers except that one intact *Coluber constrictor* was recorded and a terrapin was observed feeding on a dead fowler's toad, *Bufo woodhousei fowleri.* The frequency of occurrence suggested that feeding on dead animals occurred with considerable regularity (Table III).

The average volume % of the major groups varied somewhat during the season, May to October (Figure 1). The more detailed analyses within certain major groups, however, showed a greater seasonal variation of families and genera represented. Seeds of plants which bear fleshy fruits were particularly abundant in the spring when *Rubus* spp. and red mulberry *Morus rubra,* were predominant, and in the fall when persimmon, *Diospryos virginiana* and grape, *Vitis* spp. commonly occurred (Figure 2). The utilization of other fruits and seeds such as strawberry, *Fragaria* spp., wild plum, *Prunus* spp., and smartweed, *Polygonum* spp., was also seasonal. The occurrence of most of the seeds in the diet corresponded fairly well not only with availability of the fruit but also with maturity. Preference for ripe fruit was reported by Allard (1948) who found that the terrapin could distinguish between ripened and unripened fruit.

A seasonal variation in the occurrence of the insects in the digestive tracts was readily evident. Both immature and adult insects decreased slightly in occurrence during the season (Figure 3); this was also apparent among the more common orders of insects. The seasonal variation in Lepidoptera and Diptera, both represented mostly by larvae, accounted for the seasonal trend of immature insects in the digestive tracts (Figure 4). The relatively consistent occurrence of the adults appeared to be the result of the utilization of representatives of several orders which make their appearance at different times during the spring and summer. An examination of the occurrence of

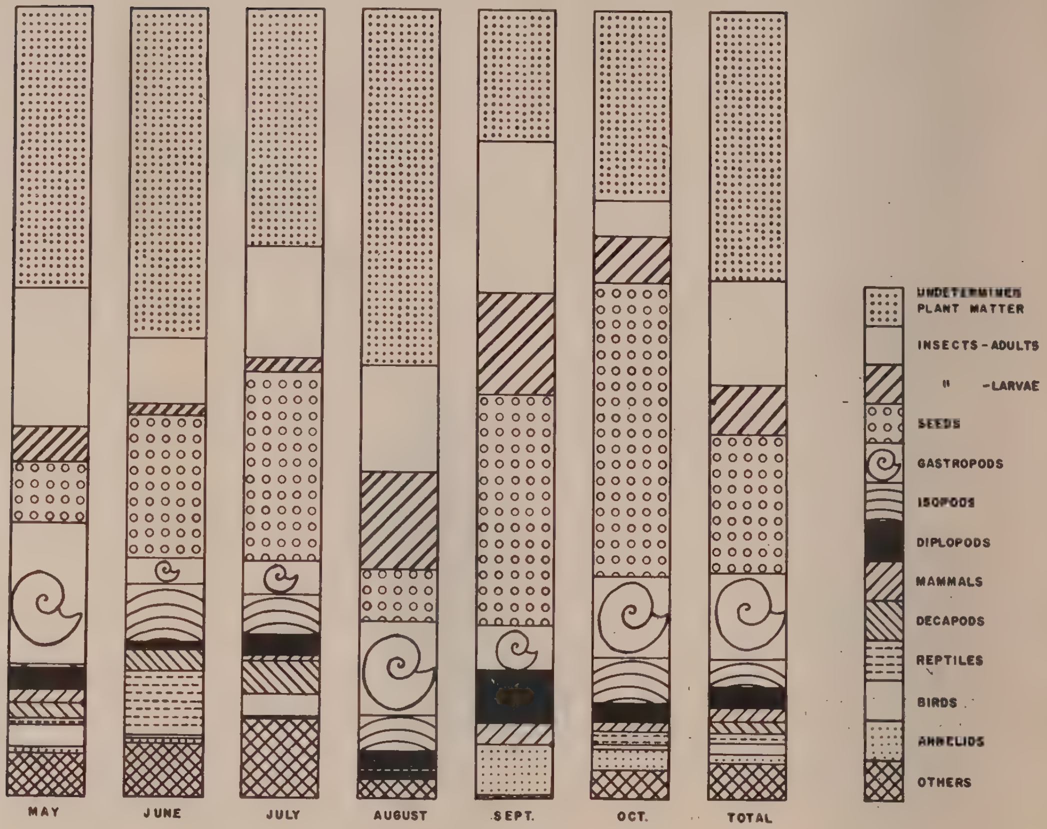

FIG. 1. Monthly and annual dietary patterns of *Terrapene c. carolina* according to percentage volume of major food groups.

representatives of the family Scarabaeidae, the most important coleopteron family, indicated that subfamilies and genera appeared in the digestive tract at definite times (Figure 5). The seasonal trend of the scarabs as a group showed a decline from spring to fall. In the spring the presence of June beetles, *Phyllophaga* spp., was most evident. *Phyllophaga,* however, were only rarely eaten in August at which time the green fig beetle, *Cotinis* sp., and the dung beetle, *Canthon* sp., were more frequently consumed. The aphodian dung beetles, in contrast, were more consistently present from June to October. It was difficult to determine if the seasonal variation in the kinds of scarabs which occurred in the diet indicated a preference by the terrapin or simply a response to availability.

Availability appeared to have been the main factor in the utilization of *Phyllophaga* in the spring and early summer. The increased occurrence of adult *Cotinis* and *Canthon* in the digestive tract in August could have been the result of an active effort by the terrapins to seek out other kinds of beetles after the pronounced decrease in the number of *Phyllophaga.* From several casual observations in the field, however, *Cotinis* and *Canthon* were most often seen in mid to late summer. If *Cotinis* and *Canthon* were common throughout the season, they probably would have been eaten in the fall as well as in the summer. It seems probable then, but not conclusive, that the utilization of the scarabs as food was the result of relative availability.

The families of gastropods, which showed a considerable seasonal variation (Figure 6), were eaten most commonly in the spring when large numbers of the limacid slug, *Deroceras* sp., and the snail, *Succinia* sp., were recorded. The importance of the slugs is further accentuated when the average frequency of occurrence is considered; an average of 3.2 *Deroceras* appeared in the digestive tracts of the 117 terrapins. During May, the average numbers of these slugs was 1.1, the greatest number found in any one terrapin being 23, while *Succinia* was represented by an average of 0.9 per terrapin, the greatest number in any

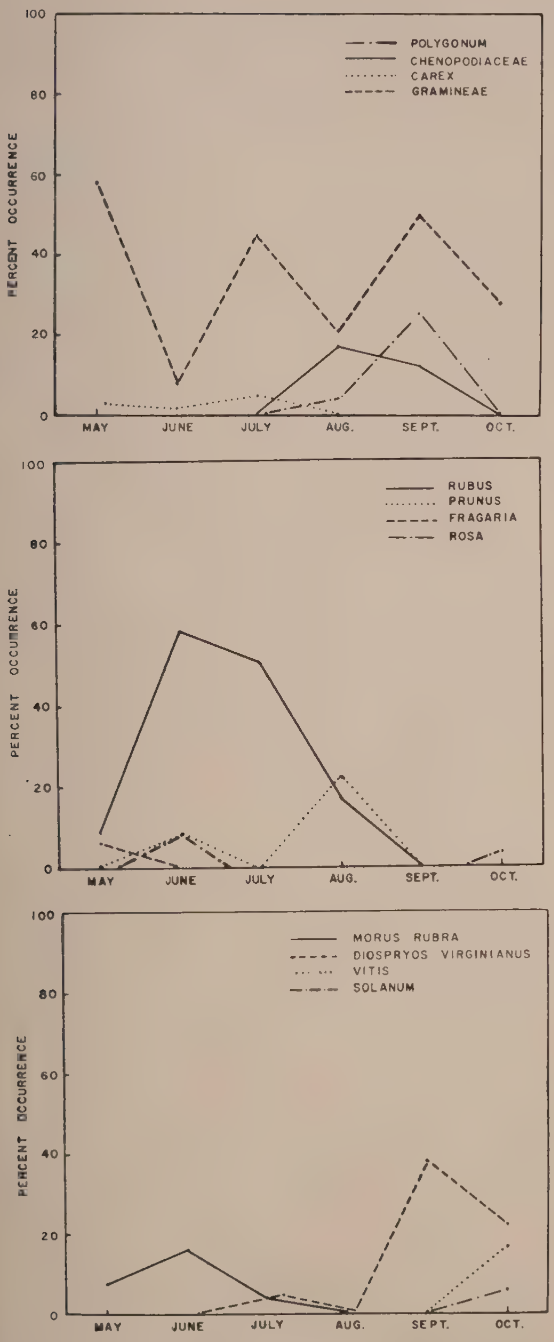

Fig. 2. Frequency of occurrence of plant materials in the digestive tracts of *Terrapene c. carolina.*

one specimen being 26. Slugs were of only slight importance after June when members of the Polygyridae and Zonitidae were more frequently eaten.

It could not be determined whether the great

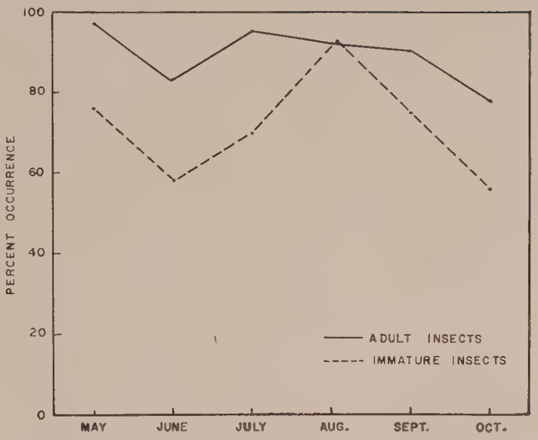

Fig. 3. Frequency of occurrence of adult and immature insects in the digestive tracts of *Terrapene c. carolina.*

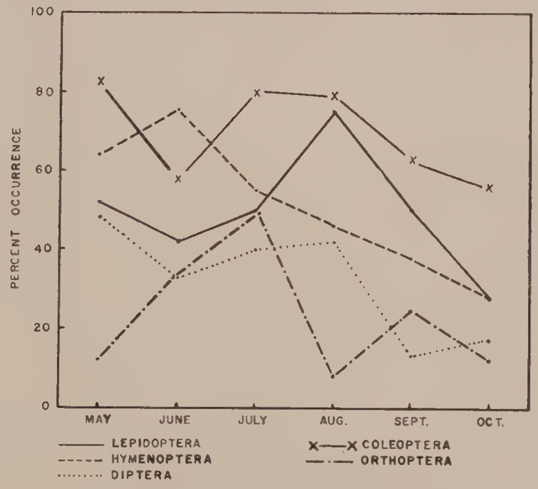

Fig. 4. Seasonal variation in the frequency of occurrence of selected orders of insects in the digestive tracts of *Terrapene c. carolina.*

numbers of *Deroceras* and *Succinia* eaten in the spring definitely reflected availability. In a study of the fluctuations in the size of a population of *Succinia,* Strandine (1941) found that the greatest numbers were present in June and July after which there was a marked decrease. Strandine suggested that high precipitation and low temperatures were the main factors which influenced the increased size of the population in spring. Because during this study *Deroceras* was found during August and September only on the edges of a ditch partially filled with water, it might be supposed that this slug also requires moist conditions. If this supposition is correct, it is possible that *Succinia* and *Deroceras* were more common in the spring. However, the area from

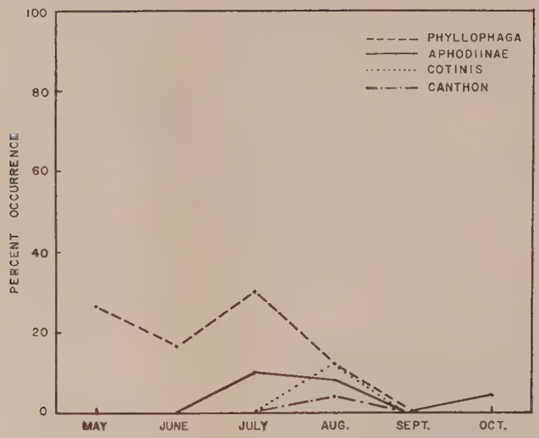

FIG. 5. The seasonal occurrence of selected members of the Scarabaeidae in the digestive tracts of *Terrapene c. carolina.*

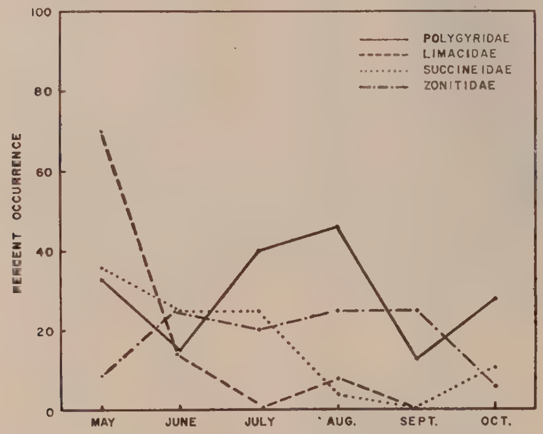

FIG. 6. Seasonal variation in the relative frequency of occurrence of selected gastropods in the digestive tracts of *Terrapene c. carolina.*

which most of the terrapins were taken was not studied in sufficient detail during May and June to determine the occurrence of these forms. During July, August and September when the fauna of the ground surface was analyzed, both *Deroceras* and *Succinia* were rare. Representatives of the Polygyridae and Zonitidae were fairly common during this period.

FOOD AVAILABILITY AND TERRAPIN UTILIZATION

The comparisons of the numbers of animals present in the environment with those utilized by the terrapin from the Carbondale Quail Research Area during the summer and fall were based on limited sampling. Some animals found in the forest floor and near logs were present in noticeably fewer numbers or were completely absent in the digestive tracts of the terrapins (Table IV). However, ratios of numbers found in the environment to those found in the terrapins illustrate discrepancies (Table V). The more significant ratios included: Formicidae 290:1, Araniae 44:1, Carabidae (adult) 23:1, Chilopoda 17:1, Acarina 11:1, Nitidulidae (Coleoptera) 11:1, Collembola 8:1, and Diplopoda 2:1. The Staphylinidae, very common in the duff of the forest floor, were completely absent in the digestive tracts examined.

TABLE IV. The relative abundance of some of the animals present in the forest floor (duff) and in the digestive tract of *Terrapene c. carolina* during July, August and September of 1956

	8m² sampled (animals/m²)	15 Terrapins examined (animals/Terrapin)
Diplopoda	0.75	0.41
Chilopoda	2.75	0.20
Arachnida		
Araneae	5.63	0.13
Acarina	6.13	0.53
Phalangiidae	0.13	—
Insecta		
Collembola	4.38	0.53
Orthoptera		
Locustidae	—	0.07
Gryllidae	0.50	—
Blattidae	0.75	—
Hemiptera		
Lygaeidae	0.38	—
Corimelaenidae	1.00	—
Pentatomidae	0.13	—
Lepidoptera		
larva	2.38	0.60
adult	—	0.13
Coleoptera		
Carabidae		
larva	—	0.13
adult	1.63	0.07
Tenebrioniidae		
larva	0.75	—
adult	—	0.27
Elateridae	0.25	—
Curculionidae	0.88	—
Staphylinidae	5.13	—
Scarabaeidae		
Unidentified larvae	0.13	0.07
Phyllophaga	—	0.13
Cotinis	—	0.27
Coprinae	0.13	—
Aphodiinae	0.50	0.20
Chrysomelidae	2.00	0.60
Nitidulidae	0.75	0.07
Buprestidae	—	0.07
Diptera	—	3.60
Hymenoptera		
Formicidae	231.75	0.80

The census of the fauna of logs confirmed the above information on the Staphylinidae and Carabidae (Tables IV and V). The absence of the large slug, *Philomycus,* the Thysanura, the Orthoptera, and several other insects in the digestive

TABLE V. The relative occurrence of some of the animals present near or in logs and in the digestive tract of *Terrapene c. carolina* during July, August and September of 1956

	Under Logs	Inside Rotted Logs	In Digestive Tract of Terrapin
Annelida	—	X	—
Gastropoda			
Triodopsis albolabris	X	—	—
Polygyra leporina	X	—	X
Philomycus caroliniensus	X	—	—
Deroceras	—	—	X
Zonitoides	X	X	X
Helicodiscus parallelus	X	—	X
Insecta			
Thysanura	X	—	—
Orthoptera			
Gryllidae	X	—	—
Blattidae	X	—	—
Coleoptera			
Carabidae	X	X	—
Tenebrionidae			
larva	—	X	—
adult	—	X	X
Elateridae			
larva	X	X	—
adult	X	—	—
Staphylinidae			
Passalidae	—	—	X
Lucanidae	—	X	—
Isoptera	X	X	—
Hymenoptera			
Formicidae	X	X	X
Lepidoptera			
larva	X	—	X

tract was evident. The common box turtle evidently did not eat typical inhabitants of the interiors of logs such as annelids, tenebrionid larvae, lucanid larvae and termites. The situation suggests that the terrapins either did not exploit this habitat or that these animals were avoided.

Although there was limited evidence that certain food items were consumed according to availability, it was obvious that many animals which were important representatives in the immediate environment were not utilized. The slow, deliberate movements of this reptile may result in an inability to capture some of the faster moving forms such as the Carabidae and Chilopoda. The fact that most of the animals which occurred in relatively small numbers in the digestive tract were eaten, suggests that they were not distasteful. However, such forms as the Staphylinidae and *Philomycus* may have been unacceptable as food.

Some of the reasons for the relative paucity in the digestive tract of this turtle of some of the animals which occurred in the duff of the forested area may lie in the sensory capacity of the turtles. The literature revealed little information on the senses of smell and taste. Carr (1952) reported that a terrapin found a fish in a burlap sack and Allard (1948) observed captive terrapins touching the food with their noses before eating; both observations suggested that the sense of smell is well developed.

The ability to hear is thought to be absent in spite of the fact that the ear is fairly well developed (Carr 1952 and Pope 1939). Latham (1916) demonstrated that the terrapin reacts readily to movements. Yerkes (1904) concluded that the perfected vision enabled the common box-turtle to judge spatial relationships. Allard (1948) observed that this animal was aware of small moving objects such as a worm or an insect but that ants were ignored. According to Walls (1942) the sense of sight is well developed; this investigator reported an efficient accommodative mechanism, a pliable lens, a very transparent dioptric medium and a retina well adapted for high resolution, having a large area, and a small ratio of visual cells to ganglion cells (2:1). The presence of retinal cells which are almost all cones indicates that this animal can distinguish colors. Walls (1942) and Quaranta and Evans (1949) demonstrated that turtles can distinguish colors of about the same wave lengths as those seen by man. Discrimination was found to be best developed in the orange-reds, less in the blue-greens and least in the blues. Walls concluded that the most important colors were orange, green, and violet. Quaranta and Evans (1949) found that Tortoises *Testuda vicina* had color preferences as orange carrots were preferred over blue-green carrots. If this preference is also shown by *Terrapene carolina,* it might explain the ability to distinguish between green and ripe fruits and the preference for the ripe fruit as recorded by Allard (1948).

Apparently, then the common box turtle must find food primarily by sight. Smell and taste, as well as sight, could be effective, however in expressing a preference. It seems possible that many forms, such as the Carabidae, Staphylinidae, Thysanura, and Orthoptera, move too quickly for this animal to catch. Other potential foods such as *Acarina* and Collembola, may be too small to be detected. However, it does not seem likely from data in Tables IV and V that size as related to Formicidae, Araniae, and especially *Philomycus* was the only factor influencing their edibility. Therefore, taste and/or smell may have been important in the acceptance or rejection of certain food items which seemingly were available to this turtle.

SUMMARY

During 1955 and 1956, 117 specimens of *Terrapene carolina* were captured in southern Illinois near Carbondale. Their digestive tracts were removed and the volume of the contents measured; individual volumes ranged from 0.5 to 65.0 cubic centimeters. The largest volumes were recorded in June after which time there was a decline until hibernation in the fall.

The contents of the digestive tracts yielded over 130 specific kinds of food. The more important food groups, according to relative volume, included: unidentified plant materials, insects, seeds, gastropods, isopods and diplopods. Earthworms, arachnids, crayfishes, and centipedes were among the less important foods. The limited evidence of vertebrates probably indicated carrion feeding habits. Some seasonal variation in utilization was indicated by the occurrence of certain seeds, insects and gastropods. The data suggested that the terrapin mostly ate foods which were readily available. However, analyses of the animals present on the forest floor indicated that there were some invertebrates which were not seen, not liked, or could not be caught by this turtle.

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REPRODUCTIVE CYCLE AND LITTER SIZE OF THE WOODCHUCK

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During an intensive study of the southern woodchuck (*Marmota monax monax* Linnaeus) on a restricted area in southcentral Pennsylvania, considerable data on reproduction were obtained. The investigation covered a 4-year period from 1955 through 1958, and revealed how the reproductive performance of the woodchuck changed from year to year in one locality. Both gross morphological and ecological data on reproduction and the reproductive cycle are presented, with emphasis on female reproductive performance. Histological data are purposely omitted in this paper, as detailed histological studies of the material will be published. This paper stresses the procedure that can be followed in obtaining reproductive data by routine gross examinations of the reproductive organs *in situ*.

Although much has been written about the woodchuck little has been published on its reproduction. Hamilton (1934) published the results of an ecological study of the woodchuck in New York state, which includes much about its reproduction and reproductive cycle in that area. Grizzell (1955) studied woodchucks on the Patuxent Research Refuge near Laurel, Maryland, and obtained reproductive data on 29 females. Rasmussen (1917 and 1918) published histological data on the ovaries and testes, but his material was inadequate during the period of hibernation, for practical reasons.

Specimens for the present study were obtained from a 10,000 acre area on the Letterkenny Army Ordnance Depot, located in southcentral Pennsylvania, 4 miles from Chambersburg in Franklin County. The depot is situated in the Cumberland Valley which, in the vicinity of Chambersburg, is a broad, gently rolling or smooth plain, with scattered rounded hills rising 100 or more feet above the valley level. The study area consisted mostly of open fields, with small mature woodlots scattered throughout. Corn, wheat, oats, forage grasses, and legumes were the predominant crops. Continuous mowing, employed to reduce the hazard of grass fires, has encouraged the growth of tender grasses, clover, and other herbs. The conditions were favorable for woodchucks and the area supported high populations. Details of the numbers in the populations are properly the subject of another publication (Snyder 1960).

METHODS

Preliminary collections of adult females were made in 1955 and 1956, but these samples were taken on only a few days of the year and during the month of April for the most part. In 1957 and 1958 the collections were spread over the entire breeding season as well as the summer and fall months. Ecological data were also obtained by trapping, marking, releasing, and recapturing woodchucks throughout 1957 and 1958.

During this period 382 adult female woodchucks were autopsied. The reproductive organs were examined *in situ* and then preserved in 10% buffered formalin. The autopsy included an examination to determine the presence or absence of corpora lutea and placental scars; the number, size, condition, and sex when possible, of the embryos and fetuses; and the condition of the nipples, mammary glands, and uterus.

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The age of each female, except for a small number trapped and marked as young of the year and subsequently recaptured when yearlings, was unknown. The young of the year were not included in this study, hence the term adult refers to females at least 10 months old. Criteria for identifying the young of the year have been worked out by Snyder (1960). The smaller size of the young woodchucks served to separate them from adults until September and October. Large young woodchucks then may approximate the weight and size of some adults. At this time the appearance of the incisors served to identify the young woodchucks. The incisors of the young of the year are narrow, long, and pointed and have not attained the brown stain that is characteristic of older animals. The points wear off and the incisors become broader with age (Snyder 1960).

The newly formed corpora lutea of woodchucks are comparatively large and distinct, and it was not necessary to section the ovaries to count them. Each one appears as a distinct bulb-like protrusion.

The embryos and fetuses were separated into two categories by visual examination: viable or dead (*i.e.,* those in the process of being resorbed). Each embryo or fetus was dissected and carefully examined to determine viability, and then preserved for histological study.

A female was considered nulliparous if there were no embryos, fetuses or placental scars. A few animals had corpora lutea, but no embryos, fetuses nor placental scars. In most instances the corpora or follicles appeared to be hemorrhagic, presumably indicative of relatively recent ovulation. These animals, with one exception, were captured between March 28 and May 4, well past the normal breeding time. They were considered nulliparous because the chances were that few of these females would have been successfully inseminated at this time (cf. below).

The Reproductive Cycle

A diagrammatic representation of the woodchuck reproductive cycle, as developed from the data gathered in 1957 and 1958, is presented in Figure 1.

Emergence from hibernation

We attempted to shoot or trap animals as soon as possible after their emergence from hibernation. The first woodchucks were observed in the study area on February 2 or February 3 in 1957 and 1958. No activity was noted during the month of January in either year. Only a few animals were active during the first week of February, but the number increased toward the middle of the month. None was trapped until February 16 in 1957 and February 11 in 1958. The absence of food material in the stomachs and intestines indicated little or no feeding during the first 2 or 3 weeks of February. Small quantities of dry grass were noted in the stomachs of specimens collected during the last week of February.

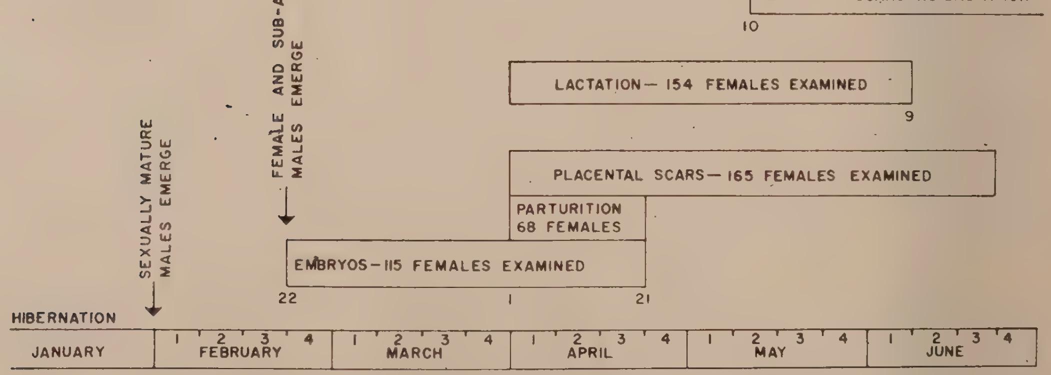
REPRODUCTIVE CYCLE OF SOUTHERN WOODCHUCK
PLACENTAL SCARS-NO LACTATION
10
LACTATION— 154 FEMALES EXAMINED
9
PLACENTAL SCARS— 165 FEMALES EXAMINED
PARTURITION 68 FEMALES
EMBRYOS-115 FEMALES EXAMINED
22
1
21
FEMALE AND SUB-ADULT MALES EMERGE
SEXUALLY MATURE MALES EMERGE
HIBERNATION
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
1 2 3 4

Fig. 1. Diagramatic representation of the reproductive cycle of the southern woodchuck.

The first green food appeared around the first of March in the form of wild onion (*Allium* sp.) and blue grass (*Poa* sp.). During February woodchucks were observed above ground only for one or 2 hours during the middle part of the day. Observation of individual animals revealed that the period spent above ground as a rule was less than one hour. A few woodchucks were shot, but most of those taken during February were captured in traps placed in the entrances to their burrows.

Only 5 of 37 animals collected between February 11 and March 2 in 1957 and 1958 were females (Table I). Males and females were taken in nearly equal numbers after March 2. The 24 males captured during February were identified as adults on the basis of criteria established by Snyder (1960). The incisors of these animals were heavily stained. Snyder (1960) found that woodchucks trapped and marked as young of the year had little or no brown stain on their incisors when captured during March and April of the year following birth. Male yearlings of known age captured during March and April also weighed much less than males captured during February. Thus, it seems that the larger males, at least 22 months old, first appeared above ground on February 2 or 3, while most of the females and sub-adult males began to make their appearance on about March 1. One cannot say whether the females and the younger males remained in physiological hibernation longer than did the older males although, with few exceptions, the females were not bred until March 1, or thereafter.

TABLE I. Sex of woodchucks collected between February 11 and March 2 in 1957 and 1958 showing predominance of males

	1957	1958	Totals
Males	15	17	32
Females	4	1	5
Totals	19	18	37

The problem of emergence from hibernation will be covered in greater detail in a later paper as more data from animals of known age are collected.

Mean date of parturition

Most of the young were born within a period of 21 days between April 1 and April 21. None of the females collected before April 1 had placental scars, while none collected after April 21 carried embryos or fetuses. Sixty-eight females were collected during the interval between April 1 and 21. Thirty of these were pregnant and 26 had placental scars. The data were analyzed using adaptations of the "Reed-Muench" method (Reed and Muench 1938) and the "graphical probit" method (Litchfield and Fertig 1941) to estimate the point at which 50% of the females had placental scars and 50% had embryos or fetuses. The 50% point was approximately April 10, the midpoint of the period when the majority of births occurred. These methods were used on the assumption that the frequency distribution of the dates of parturition is approximately normal. If this assumption is correct, April 10 was also the mean date of parturition.

Our data, as well as those of other authors, notably Hamilton's (1934), show that births do occur well outside of the period set forth above; however, our data indicate that only a small percentage of the females in a population is involved. The uterus of a female shot on May 26, 1956 contained large hemorrhagic parturitional scars and was quite distended, while 3 of 20 females collected on April 21 of that year contained small embryos. Two females collected in late February, 1957 carried embryos which would have reached term somewhat before April 1. Also, a lactating female was captured on June 28, 1958 which was well outside of the normal period of lactation.

Our records show unequivocally that the woodchuck has only one litter a year. A total of 279 females was collected for autopsy from March through October in 1957 and 1958. There were no pregnant females found after April 21 in either year, nor were any young woodchucks ever captured which could have been from a 2nd litter.

Time of insemination

Hoyt (1952) reported the gestation periods for 3 matings of the same female woodchuck as 31 days, 10 hours; 31 days, 22 hours; and 32 days. Grizzell (1955) experimented with artificial insemination and calculated a figure between 31 and 34 days. It follows, on the basis of a 31 to 32 day gestation period, that most of the sexually mature females were inseminated during the first 2 or 3 weeks of March.

Description of the mammae during and after lactation

The mammary glands and the nipples of all females were examined to determine if they were lactating and, if not, whether there was evidence of prior lactation during the current season. The nipples were considerably swollen and distended during the period of suckling and were light pink in color. The pink color and relative absence of pigmentation were probably due to the generous blood supply in the nipples and the stretching of the skin. After weaning the nipples diminished in size very slowly, so that evidence of prior lactation was discernible for at least 3 months. The epidermis of the nipples darkened and became nearly black as the mammary glands involuted. Some time later (an exact date cannot be given) the dried, darkened epidermal layer was sloughed off and the nipples became paler again. The dark pigment appeared some time prior to lactation in pregnant females.

In contrast to the nipples of pregnant or parous females, those of nulliparous females, with the exceptions to be noted, were always undeveloped and lighter in color. Some of the yearling females (known age) had darkly pigmented nipples during the breeding season. However, the nipples of nulliparous yearlings collected after the breeding season were light in color. The nipples remained somewhat distended once lactation had occurred. During the spring the nipples of most of the older females were larger and considerably more distended than those of the young nulliparous females. Presumably this difference was due to the fact that the older females had nursed a litter during the previous year.

Lactation period

Lactating females were collected from April 1 to June 9 and 154 females were autopsied during this period. In the absence of more concrete information, it was necessary to estimate the duration of lactation from the elapsed time between the point at which 50% of the births had occurred (April 10) and the point at which 50% of the females had weaned their litters. Females were judged to have weaned their young when milk was absent and evidence of recent lactation was discernible. Eight of the 15 parturient females collected between May 20 and May 26 had weaned their litters, so the point at which 50% of the parturient females were still lactating was apparently May 23. Two other estimates of the duration of lactation were obtained: (1) by counting the days from the earliest date of parturition (April 1) to the first day on which a parous female that was no longer lactating was collected (May 10), and (2) by the time elapsed from the latest date of parturition (April 21) to the last day on which a lactating female was taken (June 9). The first method gave a lactation period of 44 days, while the other 2 methods gave estimates of 40 and 48 days respectively. It appears from these data that lactation lasts approximately 44 days.

REPRODUCTION

Percentage of females pregnant

From 75 to 80% of the females were pregnant each year with the exception of 1956 when only 55.6% were pregnant (Table II). The difference in the percentage of pregnancies between 1956 and 1957 was not statistically significant ($X^2 = 3.65$, $P = 0.058$). However, the difference between 1956 and 1958 was significant ($X^2 = 9.925$, $P < 0.01$). Failure to show a significant difference between 1956 and 1957 is probably largely a matter of the small size of the sample taken in 1956.

TABLE II. Percentages of females pregnant from 1955 to 1958

	1955	1956	1957	1958
Counts of embryos and fetuses:				
No. of Females Examined	33	6	51	64
Percent pregnant	78.8	83.3	76.5	81.3
Counts of placental scars:				
No. of females examined	34	30	50	114
Percent pregnant	70.6	50.0	74.0	81.6
Combined counts:				
No. of females examined	67	36	101	178
Percent pregnant	74.6	55.6	75.2	81.5

To determine the accuracy of the figures on pregnancy, the data were divided into 2 parts. The first part consisted of data acquired when embryos and fetuses were predominant and the 2nd consisted of data obtained when placental scars were predominant. Table II shows little difference in the values calculated from the counts of embryos and fetuses made during the breeding season and those obtained by counting placental scars afterwards. The percentage pregnancy determined from counts of post-partum scars might be regarded as the most accurate, since all of these females were collected after the breeding season and had had ample opportunity to breed, assuming no shortage of males. Since there was little difference in the values derived from the 2 sources, we concluded that our collections during the breeding season were timed so that nearly all of the females had had a chance to breed. Had the samples been collected earlier the percentage of pregnancy determined from the examinations for embryos and fetuses would have been much lower than that calculated by counting scars.

Corpora lutea

The corpora lutea of pregnancy regressed slowly after parturition, and were quite distinct until the beginning of September. Their complete disappearance was first noted on September 13, and none was ever found after September 23. They still could be detected by histological sectioning, but not macroscopically.

Our evidence indicates that corpora lutea developed only from follicles that had ovulated, and that each follicle that ovulated developed a corpus lutem. The number of corpora lutea in each ovary was the same as the number of fetuses or placental scars in the ipsilateral uterine horn of the bicornate uterus in 166 of the pregnant or parous females examined. There were more corpora than embryos, fetuses or scars in 70 of the pregnant or parous females examined. The mean number of corpora lutea per female in the 70 females was not significantly larger than the mean number per female in the 166 females in which the number of corpora was the same as the number of embryos, fetuses, or scars, indicating that the excess of corpora lutea over fetuses or scars in some females was not due to an increased number of ovulations or the formation of accessory corpora lutea. Thus, accessory corpora lutea do not form in the mature woodchuck as they do in some other mammals, for example, the mare (Cole, Howell, and Hart 1931) and the mountain viscacha (*Lagidium peruanum*) (Pearson 1949). Accessory corpora lutea might be detected occasionally in histological sections of the ovaries but they certainly are not often visible to the naked eye. It follows that a count of the corpora lutea formed after ovulation reliably indicates the number of ova shed by a female each year.

Fourteen animals with corpora lutea but with neither embryos nor scars were collected between March 28 and May 4. In nearly every instance the corpora were small and the follicles hemorrhagic, which may have been indicative of recent ovulation. There was a remote possibility that some of these females were pregnant, which would explain an occasional late birth, but the majority of them probably were not successful breeders (see Fig. 1 for description of normal breeding season). The ages of these females were unknown, but in most cases they were judged to be yearlings because of their small size and unstained incisors. The failure of the animals to breed successfully might therefore be due to their having reached sexual maturity too late in the season. A more detailed analysis of sexual immaturity in yearling females will be made later with woodchucks of known age.

Many nulliparous females judged to be yearlings had ovaries that appeared grossly to have an excessively large number of corpora lutea. These small corpora could not be confused with those of pregnancy, as they are less than half the size. Preliminary histological study has shown that the cells of these small corpora lutea are indistinguishable from those comprising the corpora lutea of pregnancy, except possibly for size. However, this problem is being investigated in greater detail and will be reported separately.

Polyovulation and transmigration of the ova

The possibility of polyovulation does exist as polyovular, secondary follicles have been reported from a woodchuck collected in Pennsylvania (most likely from a young of the year) (Christian 1950). Our data would indicate that polyovulation is not a common occurrence in the woodchuck, however. The prevalence of polyovulation in immature yearlings is being studied histologically.

No instance of transmigration of the ovum was encountered during this study, as shown by the correspondence between the corpora and implantation in the ipsilateral uterine horn.

There was no significant difference in the mean number of corpora lutea in the right and left ovary, nor were there significantly more fetuses or placental scars in either the left or the right uterine horn.

Mean number of ovulations

Values were calculated for the average number of ovulations per female in which implantation had occurred (each corpus lutem representing an ovulation). These means, the standard deviations, and the number of animals examined each year to obtain them are presented in Table III. Although there were apparent differences from year to year in the average number of ovulations occurring per female in which implantation had occurred, these were not statistically significant.

Mean number of implantations

An embryo, fetus or placental scar was considered evidence of implantation, although the scar may have been post-parturient or from a resorbed embryo or fetus. Implanted embryos conceivably could have died and been resorbed without leaving a scar, but this probably does not occur (see Table IV). Should an embryo be

TABLE III. Data showing prenatal mortality at various stages between ovulation and parturition from 1955 to 1958. The number of females examined to obtain each mean is given in parentheses

Mean Value per female*	1955	1956	1957	1958
Ovulations	4.70 (47)	5.12 (17)	5.46 (71)	5.25 (102)
Standard deviation	1.37	—	1.69	1.69
Implantations	4.16 (50)	4.00 (20)	4.67 (76)	4.54 (145)
Standard deviation	1.26	—	1.41	1.25
Ova lost	0.54	1.12	0.79	0.71
Embryos and fetuses lost	0.69 (13)	—	1.25 (32)	0.57 (44)
Litter size	3.47	—	3.42	3.97
Total Prenatal mortality	1.23	—	2.04	1.28

* Only females in which implantation had occurred.

resorbed without leaving a scar the loss would be interpreted erroneously as the loss of an ovum. Scars from resorbed embryos or fetuses might disappear somewhat earlier than do post-parturient scars, but it is unlikely that this factor would have led to serious error (see Table IV).

TABLE IV. The mean number of implantations for each year determined from counts of embryos, fetuses and placental scars. The number of females examined to obtain each mean is given in parentheses

	Counts of Embryos and Fetuses	Counts of Scars	Combined Counts
1955	4.00 (26)	4.33 (24)	4.16 (50)
1956	2.80 (5)	4.40 (15)	4.00 (20)
1957	4.72 (39)	4.62 (37)	4.67 (76)
1958	4.33 (52)	4.66 (93)	4.54 (145)

The placental scars became progressively smaller during the summer and fall months and disappeared almost completely during the winter. Only 3 females examined during the spring had distinct scars from the previous year.

The mean number of implantations per impregnated female for each year was determined from the combined counts of embryos and fetuses (both viable and dead) and placental scars. A summary of these data is given in Table IV. The average number of implantations varied considerably from year to year, being as low as 4.16 in 1955 and 4.00 in 1956, and as high as 4.67 in 1957 and 4.54 in 1958. The mean was significantly higher in 1957 and 1958 than in 1955 ($P < 0.05$).

Resorption of embryos and fetuses

The amount of intrauterine mortality determined from the field collections probably was less than actually occurred, because the data were collected from females in all stages of pregnancy. Viable embryos and fetuses found in females autopsied early in pregnancy might have died later had the females survived, which would give a low estimate of the number of embryos and fetuses lost. The best estimates of intrauterine mortality are obtained from females near term, but a sufficiently large number could not be obtained at this stage of pregnancy to be able to use them exclusively for assessing prenatal mortality.

Data from 1957 and 1958 were arranged in Figure 2 as follows: The Y axis represents the number of viable embryos or fetuses per female and the X axis represents the average crown-rump measurement of the embryos or fetuses. If the number of viable embryos or fetuses per female is plotted against increasing size of the embryos and fetuses certain salient facts about fetal and embryonic resorption are revealed.

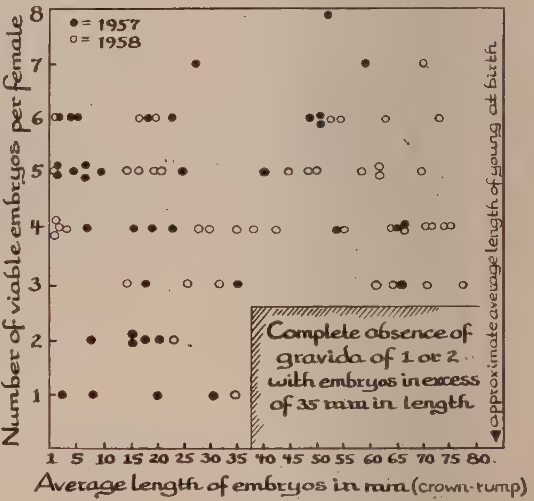

FIG. 2. The number of viable embryos or fetuses per female plotted against increasing size of the embryos and fetuses (1957 and 1958).

In Figure 2 eight of the 11 gravida[3] with less than 3 embryos or fetuses contained at least one atrophied embryo or fetus as well. None of the females with less than 3 viable embryos or fetuses had less than 3 corpora lutea, which would indicate some loss of ova in these animals. Fertilized eggs might have been lost before they were implanted and also some implanted ova might have died before they reached a stage of development that was visible macroscopically. Resorption of embryos in these woodchucks was recognized at an early stage. Two gravida with viable embryos 2 mm in length also contained necrotic resorbing placentae (the embryos were resorbed completely), which indicates that embryos had died before they reached a crown-rump length of 2 mm.

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[3] We are introducing the term *gravidum* (pl. *gravida*) to designate the total number of embryos or fetuses in a single pregnancy. The lack of an antenatal counterpart for "litter" has been a considerable handicap and has led to a great deal of confusion in the literature. The use of "pre-natal litter" is of course a contradiction in itself. Therefore, we suggest hopefully that ***gravidum*** will be used in the future to describe the ***in utero*** embryos or fetuses in a pregnancy. We wish to express our indebtedness to Dr. A. E. Wilhelmi for suggesting this term.

There were 11 females with only one or 2 viable embryos or fetuses with a crown-rump length of less than 35 mm, but no females in either 1957 or 1958 were found having gravida of one or 2 each in which fetal size exceeded 35 mm. The data indicate that females which have resorbed all but one or 2 of their embryos or fetuses early in pregnancy are quite likely to lose all of them before term. The probability of the remaining embryos or fetuses surviving beyond a length of 40 mm is less than one in 1,000 (Figure 2).

The exact ages of the females with small gravida were unknown; however, based on the criteria of age described earlier (Snyder 1960), 4 were one year old and 7 were at least 2 years old. The numbers of corpora lutea in these animals ranged from 3 to 12; the average number was 5.1. These data would indicate that excessive resorption of the embryos and fetuses was not confined to the yearling females.

Early pregnancies which were indicated only by uterine swellings or with an embryo size of less than 5 mm (crown-rump) were eliminated from the data used to estimate the percentage of embryos and fetuses lost *in utero*. This procedure did not reduce the sample size appreciably although it did omit the earliest stages of pregnancy, when death of the embryo is difficult to ascertain. The percentage of embryos and fetuses resorbed calculated on this basis was 16.6 in 1955, 17.0 in 1957, and 11.6 in 1958 (Table V). The percentage of embryos and fetuses resorbed was not significantly lower in 1958 than in other years (between 1957 and 1958; $X^2 = 1.698$, $P = 0.196$); however, these data do not take into account the extreme probability that a female with a gravidum of one or 2 embryos or fetuses will not carry it to term. If these embryos and fetuses also are counted as lost the percentage resorbed in 1957 would be 26.1 (40/153) and in 1958, 13.2 (25/190). The difference between the percentage resorption in these 2 years is then statistically significant ($X^2 = 8.515$, $P < 0.01$). We were not able to analyze the data in 1955 in this way because only 13 females could be examined for resorption.

TABLE V. Resorption of embryos and fetuses in 1955, 1957 and 1958

	1955	1957	1958
Females examined	13	32	44
Viable embryos and fetuses	45	127	168
Resorbed embryos and fetuses	9	26	22
% resorbed embryos and fetuses	16.6	17.0	11.6

Partial or complete resorption of a gravidum was observed in 7 out of 26 females in 1955, one of 6 in 1956, 13 of 39 in 1957, and 12 of 52 in 1958. It is quite evident that if resorption occurs in a female woodchuck, it frequently involves all embryos or fetuses. Ten of the 13 pregnant females in which resorption was detected in 1957 and 7 of the 12 pregnant females with resorbing embryos and fetuses in 1958 had lost all or all but one or 2 of their embryos or fetuses at the time of autopsy. Factors causing intrauterine mortality are probably intricately involved with the maternal physiology and not with the individual embryo or fetus.

Possibility of stillbirths and abandonment of the young

A few animals in 1957 and 1958 had placental scars of the season and undeveloped nipples (indicating that they did not lactate that year). These females may have lost fetuses *in utero* or the fetuses may have been born dead. There is also the possibility that the young were abandoned by the female after birth. Only the first possibility can be detected by gross examination and then only if the females are examined during pregnancy.

The following procedure was employed to determine how these animals might have lost their young or fetuses: One female in 1957 and 5 in 1958 exhibited complete loss of their gravida at the time of autopsy. In addition, 9 females in 1957 and 2 in 1958 had lost all but one or 2 of their embryos or fetuses at the time of autopsy. We have already pointed out that the probability is less than 1/1,000 that these females would have carried the remaining embryos or fetuses to term. These animals would have had placental scars and undeveloped nipples if they had been collected after the breeding season. It is only necessary to compare the percentage of such animals in the post-breeding samples with the percentage of pregnant animals which had lost their entire gravida (including animals with only one or 2 viable embryos or fetuses as well as all resorbed embryos or fetuses) to determine whether there was appreciable post-natal loss. One would expect the percentages in both cases to be about the same if stillbirths and abandonment of the young were not a frequent and added cause of mortality.

This comparison is presented in Table VI. The 2 methods, gross examination of pregnant females during the breeding season and checking for evidence of lactation and placental scars after the breeding season, gave similar values for the percentage of females with complete loss of their gravida or all of their young after birth. These procedures also gave nearly the same values in regard to the percentage of young involved in such losses. On the basis of this indirect method of analysis, it is likely that the animals with placental scars, but with no evidence of prior lactation, had lost their fetuses *in utero*. Thus, it is probable that few woodchucks abandoned their young at birth and that prenatal mortality was largely the result of intrauterine resorption.

TABLE VI. Data concerning the number of females with total gravidal loss+ and the percentage of embryos and fetuses lost in this manner (1957 and 1958)

Period loss was detected	1957		1958	
	% Females involved	% of Embryos and fetuses involved	% Females involved	% of Embryos and fetuses involved
Breeding season...	25.7(39*)	19.6(184°)	13.5(52*)	9.3(225°)
After breeding.....	18.9(37*)	13.5(171°)	5.4(93*)	4.4(433°)

* Number of pregnant females examined.

° Total number of embryos, fetuses or placental scars which were counted.

+ Total gravidal loss = complete loss of all embryos or fetuses *in utero* in a given pregnancy.

Total prenatal morality

Total prenatal mortality in this woodchuck population was heavy, especially in 1957. Referring back to Table III, we find that the loss between ovulation and parturition in females with evidence of implantation was 24 to 37 % of the ova shed.

Average litter size

It is a common practice when describing the biology of an animal to report the average litter size. Average litter sizes are often calculated from data collected over a period of time and from a variety of localities, so that they are relatively meaningless. Density, age composition and other factors of the population which might influence the size of the gravidum or of the litter are rarely taken into account. In many cases the figure given is not the true size of the litter at birth, but rather the average number of fetuses per gravidum or the average number of placental scars per female or a combination of both. A tally of placental scars, unless it is made very soon after parturition (*i.e.,* when resorption scars can be distinguished from post-parturient scars), gives no indication of the incidence of intrauterine mortality. Counts of fetuses can be used to calculate a reliable index to the true litter size at birth only if a sufficient number of animals are examined throughout the breeding season and if the prevalence of intrauterine mortality as revealed by the presence of atrophied embryos and fetuses is accurately determined.

The average litter size is defined in this paper as the average number of post-natal living young produced per pregnant female. The term is an abstract one which takes into account all prenatal losses, so far as they can be determined. If one included only those females which produced living young, the value for the average litter size would be quite different from the value calculated from prenatal data. The term "average litter size" is useful only as an expression of the productivity of the breeding females in the population and would be quite meaningless if all prenatal losses were not taken into account.

An estimate of the true litter size at birth was computed as follows for each year with the exception of 1956. The mean number of implantations per breeding female determined from counts of embryos, fetuses and placental scars was used as the starting point. From this figure was subtracted the average loss of embryos or fetuses per pregnant female. For example, the mean number of implantations in 1958 was 4.54 and the loss between implantation and parturition was 0.57 embryos or fetuses per female. The litter size at birth was then approximately 3.97. The true litter size was somewhat smaller than this because the highest resorption rate detected must be below the true value. The approximate litter size was 3.47 in 1955 and 3.42 in 1957 (number of viable embryos or fetuses per gravidum ranged from one to 8). The estimate of the average litter size in 1955 was not as good as those obtained in 1957 and 1958, because the percentage of embryos and fetuses resorbed was determined from only 13 specimens.

Reproductive rate

The reproductive rate, the number of young born per female in the population, is perhaps the best expression of the productivity of a population, because it takes into account the percentage of pregnancy as well as the average litter size. This value is determined by multiplying the mean litter size by the percentage pregnancy. The birth rate, the number of young born per animal in the population, is exactly one-half of the reproductive rate, if the sex ratio in the population is one to one.

The terms, reproductive rate and birth rate, are used in this paper to express the productivity of the breeding population. Reproductive rate and birth rate are sometimes used as measures of the productivity of populations of animals that breed throughout the year and, when used in this way, an average population size for the year is calculated. The problem is simplified when dealing with woodchuck populations, as there is only one breeding season per year, and the females have only one litter of young each year. Thus, the rates apply to the number of animals in the population when the young are born, or more specifically to the breeding population.

Reproductive rates were 2.59 in 1955, 2.57 in 1957 and 3.24 in 1958. The improvement in the reproductive performance of this population in 1958 is expressed quite clearly by these values. Each female in 1958 would add almost 0.70 more young to the population than would a female in 1955 or 1957. Whether or not this improvement would be reflected in increases in the size of the population would depend entirely upon mortality factors acting on the population.

Litter size of yearling

Only a portion of the females reach sexual maturity and bear a litter at one year of age. Information was obtained on 15 yearling females of known age. These animals were tagged as young of the year in 1957. Eight of these (53.3%) were pregnant in 1958 at the end of their first year. The number of embryos, fetuses, or placental scars ranged from 2 to 4 per gravidum, the average being 3.13. The average size of the gravidum of yearlings was thus much smaller than that of the older females.

The fetal sex ratio

The internal reproductive organs become distinct and one can differentiate the sex of the fetuses accurately without optical aids when the crown-rump measurement reaches 50.0 mm. The fetal sex ratio, based on 170 individuals with a crown-rump measurement of 50 mm or more, was 84 males to 86 females.

DISCUSSION

The ultimate litter size at birth depends upon the number of ovulations and the magnitude of prenatal mortality, whereas the reproductive rate, an expression of the population's productivity, depends upon the litter size and the percentage of pregnancy. Changes in any of the factors affecting these values will be reflected in the population's reproductive performance. We were able to obtain enough data to show significant differences from year to year in the mean number of implantations, in the percentage of embryos and fetuses resorbed and in the percentage of females pregnant. The mean number of ovulations was lower in 1955 than in 1957 and 1958, but the difference was not quite significant. However, since loss of ova was substantially the same each year, the significantly lower mean number of implantations in 1955 must have been a reflection of a lower average number of ovulations per female. A larger number of females were included in the samples of females with evidence of implantations, because placental scars remain after corpora lutea have disappeared. Statistical treatment in this case was a matter of sample size.

Changes in the average litter size and the reproductive rate appear to have been mainly the result of changes in the ovulation rate, the percentage of females pregnant and the percentage of embryos and fetuses resorbed. It should be kept in mind, moreover, that slight changes in certain factors may in combination affect a definite change in the litter size or reproductive rate.

The reproductive performance of this population was much improved in 1958 after 3 consecutive years of rather low productivity. Reproduction in 1956 was decidedly lower than in other years. We were unable to acquire sufficient data to compute an estimate for the average litter size for this year, but the reproductive rate must have been very low since only 55.6% of the females examined were pregnant. The results of this investigation emphasize the need for intensive studies to determine the factors responsible for these variations in the reproductive performance of populations.

SUMMARY

From 1955 to 1958 the reproductive organs of 382 adult female woodchucks from a 10,000 acre area in southcentral Pennsylvania were examined to obtain information about reproduction and the reproductive cycle.

The sexually mature males emerged from the hibernation dens around February 1 in this local-

ity, about 3 to 4 weeks before the females and the sub-adult males. The majority of the sexually mature females were inseminated during the first 3 weeks of March and most of the young were born during a period from April 1 to April 21, the mean date of parturition being approximately April 10.

From 75 to 80% of the females were pregnant each year, except in 1956 when only 20 of 36 examined were pregnant. The collective noun *gravidum* (pl. *gravida*) has been introduced to describe the total number of embryos or fetuses in a pregnancy. Gravidum is considered to be a prenatal counterpart of litter. The mean number of implantations per gravidum varied considerably from year to year, being as low as 4.00 in 1956 and as high as 4.67 in 1957. The percentage resorption of embryos and fetuses declined from 16.6 in 1955 and 26.1 in 1957 to 13.2 in 1958. The approximate average litter size was highest in 1958, 3.97 compared to 3.47 in 1955 and 3.42 in 1957. The reproductive rate increased from lows of 2.59 in 1955 and 2.57 in 1957 to 3.24 in 1958.

ACKNOWLEDGMENTS

The investigation was supported in part by Grant H 2489 from the United States Public Health Service. The field research was directed in part by David E. Davis. The woodchucks were collected on the Letterkenny Army Ordnance Depot under an agreement with the U. S. Army. Colonel William F. Rader, Commanding Officer of the depot, contributed his support to the project. Mr. Thomas Hawthorne, Deputy Chief Security Officer, assisted the project personnel with many phases of the field work.

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A QUANTITATIVE STUDY ON THE ACTIVITY OF THE DUSKY SHREW (*SOREX VAGRANS OBSCURUS*)

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INTRODUCTION

Although considerable work has been done on the various species of American shrews, studies of their behavior patterns and especially of their daily rhythms of activity have largely been neglected. A study of such phenomena, however, may give valuable information concerning the niche of the animals in a community, and an appreciation of their peculiar physiological problems. The present paper is an attempt to analyze the daily activity of the dusky shrew (*Sorex vagrans obscurus* Merriam) under summer conditions at 7000 feet altitude in the Sierra Nevada Mountains at Huntington Lake, Fresno County, California. Most of the work was done in June, July, August and September of 1958 and 1959, although the study was continued throughout the winter months with 2 shrews at Fresno, California (elevation 270 feet).

The first detailed accounts of the activity rhythms of shrews were those by Crowcroft (1954), (1957). These works on European shrews have been used as a basic guide for the present studies.

The author wishes to thank Dr. Peter Crowcroft for his valuable suggestions on the manuscript.

METHODS

Twenty captive animals of undetermined sex and age were used in these observations and experiments. All were captured in Sherman live traps set under a large fir log in a wet meadow; less than 100 feet from the place where the shrews were kept as captives out of doors under a dense clump of small firs. Other observations and experiments on free-living shrews were made under or beside the same log at various times in June, July, or August but over a period of 3 years.

The cages used were of 3 types each with nesting material and with containers for food and water. One type had 96 square inches of floor space. The sides were made of plexiglas, but the floor, ends, and half of the top were of wood. The other half of the top was screen in order to assure adequate ventilation. This cage proved best for direct observations. A 2nd type of cage simulated natural conditions. It was constructed of wood. Its sides and ends were lined with tin plate 14 inches high. This cage had no top and presented no problems of temperature or humidity. Its 7 square feet of floor were covered with rotting wood, litter and soil containing growing plants taken from the environment of the shrews. A 3rd type had 288 square inches of floor. Its sides and top were of screen wire. A 15-watt electric lamp was installed inside at one end. A slightly larger light-tight but air conditioned box could be inverted over the cage and the light thus controlled.

Water bottles and food beakers were allocated in the cages in such a way that the animals would have to cross a treadle switch to reach them. The switch was connected with a 12-volt battery and an electromagnetic recording apparatus. Clothier (1955) found 4.7 grams to be the mean weight for this species in Montana, but it increased to 7.2 grams as they approached sexual maturity. The treadle switch, therefore, was adjusted to close with a weight of 3.5 grams. The recording apparatus consisted of an alarm clock modified to drive a disk bearing a circular paper 18.5 cm in diameter. The periphery of the paper was marked off into 12-hour segments, each segment containing 6, 10-minute units each 9 mm long. These papers carried the record of activity as dots made along its periphery by the electromagnet. They were changed daily at 7 A.M. and 7 P.M., Pacific Daylight Time. After each paper was removed from the apparatus, the dots occurring in each 10-minute interval were counted with the aid of a lens. These were recorded on coordinate paper representing the 10-minute intervals of night (7 P.M. to 7 A.M.) or day (7 A.M. to 7 P.M.). If the dots in a 10-minute interval were more numerous than 10, they were nevertheless recorded as 10 because larger numbers could not be counted accurately and the chances for error increased. Hence the lower numbers are more accurate than the 10 which actually may represent many more contacts. Crowcroft (1957) used a similar method of recording activity and points out that, "this kind of error tends to smooth out rather than exaggerate differences and any differences which do emerge are sure to be valid ones."

Food was renewed daily at 7 A.M. and 7 P.M. It was constantly available. The food formula described by Pearson (1950) was modified to include an equal part of water-soaked oatmeal with the hamburger and Purina dog food. It was kept frozen until fed.

Three or 4 days were allowed for an animal to become accustomed to the new cage and surroundings before its activity record was started. Three animals with about the same weights (nos. 2, 3, and 8) were selected and their activities were recorded for 16, 9, and 12 days respectively or for a total of 37 consecutive days. Two shrews were taken to Fresno, California, in September, 1958 and kept until May 1, 1959 after which their activity was recorded for a total of 26 days.

In order to test the effect of changing "night" and "day," shrew no. 20, was placed in darkness by covering its cage during the daylight period. It was subjected to light from a 15-watt electric lamp within its cage, during the night. The diffused noon-day light within the cage was 13-foot candles. The electric lamp at night gave 10-foot candles. When the lamp was used, the temperature inside the cage was less than 2°F above the outside temperature. The relative humidity inside was only slightly more than when the cage was uncovered. This experiment was continued for 20 days. The first 9 days were used to allow the animal to become accustomed to the "reversed" conditions. Its activity was then recorded for 6 days after which the animal was exposed to natural daylight and darkness for a 5-day period when another record was made.

In order to compare the activities of the caged shrews with free-living shrews, the recording apparatus was moved twice (fall 1958 and spring 1959) to the log where 8 of the shrews previously had been captured at intervals ranging from 3 to 7 days. The treadle switch was placed inside a small wooden box with holes large enough to admit a shrew (but not a mouse). The box was so arranged that any shrew running the full length of the log would have to go over the treadle and its passage would thus be recorded. The box was then baited and placed under the log at the exact place where a shrew (no. 8) had just been trapped. Three days later when activity began to be recorded the bait was removed. After sufficient records had been obtained, a shrew (no. 9) was caught. The trap was reset but did not yield another shrew (no. 10) until 7 days later, suggesting that only one shrew (no. 9) was responsible for the records obtained. The next spring (1959) the activity of another wild shrew was recorded in a similar manner under the same log.

An uninterrupted series of one or more 10-minute periods of activity is defined here as an "activity period." A "rest period" is a similar period of a series of 10-minute periods showing no activity. "Day" is 7 A.M. to 7 P.M. and "night" is 7 P.M. to 7 A.M. Pacific Daylight Time except for the study made at Fresno which was made on Pacific Standard Time.

RESULTS

The sum of 37 days of activity involving 3 caged shrews (nos. 2, 3, and 8) is shown in Figure 1.

There were from 9-15 activity periods daily for all the captive shrews and for the 2 wild shrews. Three captive shrews showed some variation in the number of activity and rest periods at night. Shrew no. 2 had an average of 6.9 nocturnal rest periods with a standard deviation of 1.9; shrew no. 3 averaged 7.4 with a standard deviation of 1.4; and shrew no. 8 averaged 8.3 with a standard deviation of 2.3. Although the shrews fed from only 2 to 4 times during each activity period, they were actually continuously exploring all parts of the cage. Crossing the treadle switch 60 or more times during an hour of activity was not uncommon. Such continuous activity, however, was interspersed with little naps 30 to 70 seconds long when the animal stopped, rested its nose on the ground—sometimes twitching its vibrissae, sometimes even turning completely around but usually with its eyes closed and apparently sleeping lightly.

The 8-day records of the free-living shrews under the log rarely showed more than 2 contacts (one in and one out of the box) for each visit. These visits were apparently made only once during an activity period. The number of activity periods for these unrestrained shrew for day and night were well within the ranges of those made by captive shrews.

The number of 10-minute periods, of the 72 periods for each day and night, which showed some activity, was recorded for 3 captive shrews (Table I).

The 2 free-living shrews utilized 36 of the 10-minute periods for both day and night.

Some activity periods were represented by a single contact. Data pertaining to the length of activity periods and rest periods for 3 captive shrews for a total of 37 consecutive days are shown in Table II.

A coefficient of activity as suggested by Szymanski (1918) was also determined for 3 captive shrews. This coefficient of activity is obtained by dividing the number of 10-minute rest periods into the number of 10-minute activity periods.

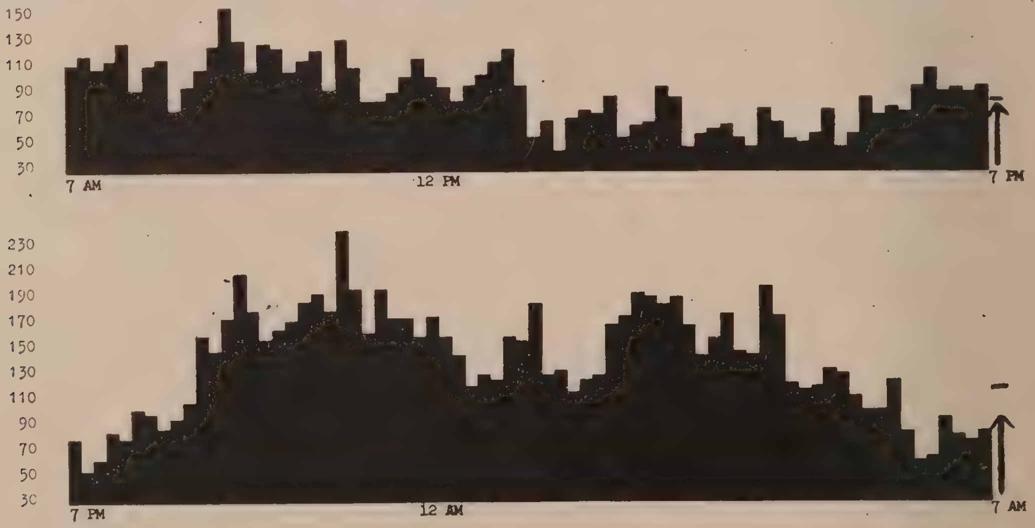

FIG. 1. Showing daily rhythm of activity for 3 shrews for a total of 37 days

TABLE I. The number of 10-minute periods utilized in each 12 hours (72 periods) by shrews nos. 1, 2 and 8

Animal's Number	Range during day	Range during night	Average during day	Average during night
2...........	22-41	43-57	30.0	50.4
3...........	22-35	27-53	30.2	45.7
8...........	19-42	19-56	30.4	37.5

This number for 3 shrews totaling 37 days of activity was 0.65 for the day, 2.01 for the night or 1.18 for the 24 hour period. In order to compare night and day activity and to compare this species with other shrews, a night-day ratio was obtained by dividing the number of electrical contacts recorded during the night by those recorded for the day. These night-day ratios for 3 shrews were: shrew no. 2, 1.48; shrew no. 3, 1.18; and shrew no. 8, 1.38. The average for all 3 shrews for a total of 37 days of activity was 1.38. The 2 shrews that were kept all winter in Fresno had a night-day ratio of 1.27 when tested for 26 consecutive days in May.

TABLE II. Length of activity and rest periods for day and night for 3 shrews (nos. 1, 2, and 8) for a total of 37 days

	Daytime (7 A.M.-7 P.M.)	Night (7 P.M.-7 A.M.)
Longest activity period	3h, 20m	4h, 40m
Longest rest period	3h	2h
Average activity period	42m	58m
Average rest period	45m	38m

The free-living shrews had a night-day ratio of activity of 1.10. Shrew no. 20, that was used in the night-day "reversal" experiment, had an average night-day ratio of 2.08, the highest of all the shrews studied.

When this shrew was subjected to 9-days of reversal of light and darkness during the night and day respectively, the night-day ratio dropped to 0.46. When natural light and darkness were restored for 5 days its ratio returned to 1.39. The temperature and humidity were nearly the same inside the cage as they were on the outside.

DISCUSSION AND CONCLUSIONS

Reference to Figure 1, and Tables I and II, shows that the dusky shrew is more active by night than by day, but that there may be activity at any time during a 24-hour period. There is a low morning peak of activity which declines gradually until it reaches the nadir between 3 P.M. and 5 P.M. The slight rise at 6 P.M. is followed by another depression at 7 P.M., after which the nocturnal activity culminates in 2 major peaks centering about 9.30 P.M. and 3 A.M., between which is another lesser peak. Neither the lesser peak about 1:00 A.M., nor the depression about 7:00 P.M. are considered "real" since peaks and depressions of magnitude as great can be observed at various places along the histogram. Perhaps this peak and depression result from the fact that the 3 shrews differ in their number of rest periods during the night. This would result in their activity and rest periods coinciding occasionally to elevate or depress the cells of the histogram.

The histogram (Fig. 1) is similar to that shown by Crowcroft (1954) for the European common shrew (*Sorex araneus*) in that the first major nocturnal peak is larger than the last one. The low morning peak and the afternoon depression are shared by both species.

Light seems to be the regulating factor in the 24-hour rhythm, because an activity pattern can be fully reversed by lighting the cage at night and darkening it by day, as conditions of food, temperature and humidity remain unchanged.

At present, explanations are lacking for the cause of peaks of activity and the afternoon depressions.

They may possibly correlate with the availability of food or the presence (or absence) of enemies. As a stimulus for further investigation it might be proper to speculate on what appears to be a close correlation between shrew activity and the presence of certain food and enemy species. These apparent correlations of activity of the prey and the predator may, however, be incidental or coincidental rather than causal. For instance, in July the morning peak corresponds with the emergence of the imagines of certain tipulids used as food by this shrew. Possibly high humidity or other physical factors actually activate both the shrew and the insect. The afternoon depression occurs during the warmest part of the day when shrew activity is lowest and may actually be stimulated by the higher temperature or lower humidity, which permits the food species (insects and arachnids) to be more active, and perhaps less available. During this part of the day also the predatory steller jays (*Cyanocitta stelleri*) visit the edge of the meadow to catch insects (and possible shrews). They are never seen hunting there during the cool mornings when the dew is on the tall forbs, grasses, and sedges (when shrews are active).

The first major peak of nocturnal activity begins at about the same time the wet wood termites (*Zootermopsis nevadensis*) begins to emerge from rotting logs to fly to new locations. This species, which flies almost every evening in July and August is an important food species in the summer diet of the dusky shrew. The termite begins its evergence about the time the cool down-mountain breeze starts each evening. It is possible that the air movement, sudden drop in temperature, or failing light may be the stimulus that starts the activity of the shrews and the insects at the same time. The last major nocturnal peak corresponds with the lowest daily temperature when the insects, spiders and phalangids are inactive and are probably more available because some of these species (certain spiders) are known to move down from the higher vegetation to spend the night in the litter around the lower forbs and sedges.

From 9 to 15 activity periods daily are required by the dusky shrews to meet its high nutritional requirements. The longest activity periods occur during the night, and the longest rest periods during the day.

It is noted that the average number (30) of 10-minute periods for the day was about the same for 3 captive shrews but these showed considerable variation in the average for the night and for the difference in the number between day and night (Table I). A possible explanation for the equal number for the day might be that daytime activity is minimal and, since the shrews were nearly all of the same weight, their minimal diurnal requirements would be about the same. The variations in the range of activity at night may involve unknown factors such as sex or age.

The rhythms of activity are apparently caused by nutritional requirements or by the physiological changes resulting from them. The short naps enable the shrew to continue its high activity level and rapid expenditure of energy throughout an activity period. Crowcroft (1954) observed these naps in the European common shrew (*Sorex araneus*) and called them "shorter-term rhythm." The night-day ratio of 1.27 for 2 shrews kept in Fresno for 8 months indicates that the basic behavior patterns of this species are stable under greatly varying conditions.

In exhibiting greater nocturnal activity the dusky shrew resembles the European common shrew but differs from the European pygmy shrew (*Sorex minutus*) which has a night-day ratio of activity of only 0.88 (Crowcroft 1957). The average of 1.38 for the night-day ratio of *Sorex vagrans* is essentially the same as found by Crowcroft (1957) for the European common shrew (*Sorex araneus*) and suggests similar niches for the species.

The Syzmanski coefficient is 1.18 for the dusky shrew which is less than that found by Crowcroft (1954) for *Sorex araneus* (1.46) and *Sorex minutus* (1.36).

SUMMARY

1. In summer the daily activity rhythm of the dusky shrew is characterized by 2 major nocturnal peaks, a lower morning peak and an afternoon depression. Parts of this curve may correlate with the availability of food and the presence or absence of enemies.
2. Light is the regulating factor responsible for changes in the 24-hour rhythm. An activity pattern can be reversed if light is applied in a light-tight cage during the night and darkness during the day, with the temperature, and humidity unchanged from the outside.
3. Within the daily pattern is a "short-term rhythm" involving from 9 to 15 activity periods daily alternating with rest periods. This "short-term" activity is apparently caused by physiological requirements connected with nutrition. Even these "short-term" activity periods are interspersed with short naps which enable the shrew to adjust its physiology to its rapid expenditure of energy.
4. The Szymanski coefficient of activity for the dusky shrew is 1.18 and is somewhat less than that recorded for European shrews.
5. The average ratio of night-day activity of 1.38 for the dusky shrew is nearly identical with that of the European common shrew.
6. Eight months of captivity produced no discernible changes in the basic daily patterns of activity of 2 dusky shrews kept at lower elevations under a variety of seasonal conditions when compared with those of recently captured shrews or with unrestrained wild shrews.

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BURROWING ABILITY AND BEHAVIORAL RESPONSES TO DESICCATION OF THE SALAMANDER, *PLETHODON CINEREUS*

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Plethodon cinereus is a lungless, thin-skinned amphibian and is unusually dependent on the moisture of its environment for maintaining water balance and keeping the skin functional as a respiratory organ. Its completely terrestrial mode of existence brings it in contact with unfavorably dry situations and, during drought, the survival of individuals in the forest floor might be contingent on their ability to penetrate the mineral soil and reach a moister environment. This is particularly true if cover such as logs, sticks, and stones is lacking.

Cochran (1911) and Test and Bingham (1948) have reported this species below the soil surface the latter authors suggesting that a large proportion of the population may be underground at any given time. Grizzell (1949) found *P. cinereus* hibernating about 90 cm below the surface of the soil.

Burrowing is not the only way in which salamanders might enter the mineral soil, as earthworm tunnels, burrows of small mammals, and cavities left by decayed roots are commonly present. However, a burrower has the advantage of being independent of such routes.

METHODS

Three experiments were carried out. The first was designed to test burrowing ability of *P. cinereus* in sand; the 2nd was extended to include additional substrates. The 3rd tested ability to enlarge pre-existing holes in substrates in which burrowing was difficult or impossible. In all 3 experiments, observations on behavioral responses other than burrowing were also made.

The laboratory in which experiments 1 and 2 were carried out was a basement room lacking windows and functional air inlets. The door was kept closed except when I entered or left the room. A recording hygrothermograph beside the experimental containers registered a range in relative humidity of 22-58% and a temperature range of 15°-21°C during these 2 experiments. The greatest difference between maximum and minimum for any one day was 1.5°C in temperature and 16% relative humidity. The humidity above the moist substrates in the containers was undoubtedly higher than these values during the early part of the experiment, decreasing to that of the room after the substrate dried. Natural light was entirely excluded from the room. Experiment 3 was conducted in a well-lighted, ventilated laboratory.

With the exception of humus, substrates were taken from a beech-maple forest near Carp Lake (Emmet Co.), Michigan, where *P. cinereus* was abundant. Humus was taken from a hardwood swamp near Ann Arbor, Michigan.

Experiment No. 1

Two glass terraria each 25 cm long, 20 cm wide, and 30 cm high were used. In the bottom of one, I placed 3 cm of loose, wet leaf-fragments from the F layer. Two cavities 5 cm in diameter and 1.5 cm deep were excavated in this. Each cavity was then covered with a small piece of glass. On top of the fragments and glass plate I spread a layer of wet sand 3 cm thick, leaving a small space uncovered at one end of each piece of glass. Through these spaces I inserted flexible tubes of polyethylene, each 7 cm long and with an inside diameter of 1 cm. The ends of the tubes were pushed just under the glass, and then wet sand was filled in around them. The tubes inclined approximately 45°, and formed artificial burrows leading from the surface of the sand to the cavities. Hereafter this terrarium will be known as A.

A 2nd terrarium was prepared in the same manner as the first, differing from it only in that no cavities or plastic tubes were present. This will be called B.

Two pieces of bark each about 15 cm x 8 cm were placed on the sand in each terrarium. In container A the mouths of the tubes opened beneath the pieces of bark. An individual of each of the color types of *P. cinereus* was introduced into each terrarium. Their measurements (snout-front of hind leg) were 33 mm (red type) and 37 mm (black type) for container A, and 35 mm and 42 mm, red and black respectively, for container B. The experimental containers were covered with a double layer of cheese cloth held in place by a rubber band. An electric light on the ceiling directly above them was, with a few exceptions, turned on between 8:00 A.M. and 10:00

A.M. and off again between 7:00 P.M. and 9:00 P.M.

Locations and positions of all salamanders were recorded several times each day, both during periods of light and of darkness. Night observations were made by red light. When necessary, the pieces of bark were lifted to ascertain a salamander's position.

The experiment was in progress from November 18, to December 10, 1957.

Experiment No. 2

A series of 5 containers of similar size to those of experiment 1 were prepared. They will be known as C through G. Cage C differed from A of the previous experiment only in that pieces of bark were not present. Similarly, lack of bark in D was the only difference between it and B of experiment 1. Container E was filled to a depth of 6 cm with a layer of leaf-fragments heavily bound together by rootlets, the mass being cut so as to fit snugly in the terrarium. Cage F had a layer of humus 6 cm deep with only occasional rootlets. In container G, I placed a 3 cm layer of leaf-fragments bound with rootlets. In this material 2 depressions 5 cm in diameter were excavated and a salamander placed in each. The cavity was then covered with fragments followed by a layer of sand 3 cm thick over the entire surface of the container. None of the containers in this experiment contained bark.

There were 2 salamanders per container. Although those of container C were placed in depressions in the leaf-fragment layer before the sand was added on top, within 10 minutes after the cage had been prepared they had crawled through the plastic tubes onto the surface of the sand. With the exceptions of C and G noted above, the salamanders were simply placed on the surface of the substrate. All containers were covered with cheese cloth as in the previous experiment.

In an attempt to strengthen the stimulus to burrow, lights were left on continuously after the first 9 days. Prior to this they were operated as in experiment 1.

This experiment began on December 23, 1957, and was terminated for each container by the death of the salamanders inhabiting it. The last salamander died after 42 days.

Experiment No. 3

Two terraria 35 cm x 19 cm x 27 cm were used. One was filled to a depth of 6.5 cm with sand and the other to the same depth with humus. Twelve evenly spaced holes 2.5 mm in diameter were made vertically in the substrates of both terraria with a small rod. All extended to the bottom of the container. Six red salamanders ranging from 31 to 39 mm (snout-front of hind leg) were then placed on the surface of the material in each container and both terraria covered with glass. The experimental period lasted from June 29, to July 18, 1958. During this time observations were made one to 3 times daily.

In all experiments the substrates were saturated with water when placed in the containers. The materials were allowed to settle into position exercising care not to pat or pack them, although the surface was gently smoothened. Thus the structure of the substrates were made to approach the undisturbed field condition as nearly as possible.

RESULTS

Before discussing the results in terms of burrowing and behavioral responses to desiccation, several incidental observations should be mentioned which are important in interpretation of the data.

The first is the tendency of the salamanders to wander around the periphery of the container during their activity periods. This was especially pronounced in experiment 2 in which there was no bark beneath which they could go. Lumping together all observations in which animals were on the substrate rather than under bark or in tubes, it was found that during 86.3% of the observation periods, salamanders were within 1 cm of the wall of the terrarium and lying parallel to it. This was not a response to a tactile stimulus, as Test (1946) has shown a positive thigmotaxis to be lacking in this species. The reason for this localization may have been partly the result of encountering an obstacle to forward movement and attempting to circumvent it. This influenced the results obtained in container C.

Second, in experiment 1 there was very little difference in location of the salamanders when periods of darkness and light were compared (Figure 1). Therefore, all data from this experiment can be treated together as a single unit. This is surprising in view of the results of Test (*op. cit.*) who found that this species reacted to light by retreating to cover. The probable explanation is that even the normal nocturnal activity was inhibited by the unfavorable moisture conditions which were imposed on the animals.

Results of both experiments 1 and 2 indicate that *P. cinereus* cannot burrow in sand. Experiment 1 was terminated by the death of the 2 salamanders in container B (lacking tubes) on

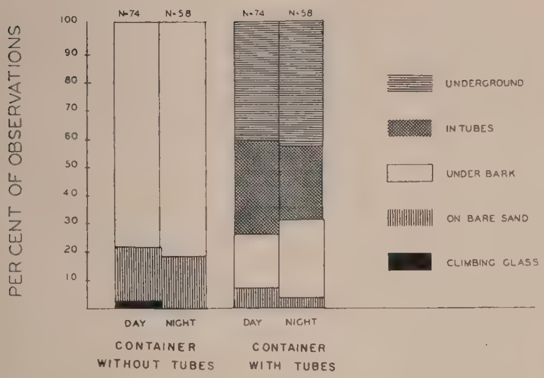

FIG. 1. Comparison of salamander locations during the day and night. Experiment 1.

December 10, after 23 days. At this time the salamanders in the cavities of container A (with tubes) were alive, moist, and glistening whereas the dead ones in B were dull in appearance. The moisture of the top centimeter of sand had decreased from 26.6 to 1.0% dry weight in A and from 26.6 to 1.3% in B. The leaf-fragments beneath the sand were still moist in both containers. The animals in container A were able to reach this moisture through the artificial burrows, whereas the salamanders in the container without tubes were forced to remain on the surface where they died of desiccation. This is attributed to inability to burrow rather than to lack of attempt to do so, in view of burrowing in other substrates discussed below.

In container A, a hole appeared in the sand on November 29, about 3 cm from a plastic tube. Subsequently it was observed to be in use by a salamander. At first this was taken to indicate burrowing in sand. However, after concluding the experiment, liquid agar was poured into the hole and excavated after it solidified. It was found that some of the leaf-fragments had been displaced, apparently during installation of the plastic tube, and that a hummock of fragments had been formed leaving only a 2 mm layer of sand above it. As the sand dried, it filtered down into the lower layer, probably aided by the movements of the salamander in the fragments just beneath. The hole was continuous with the cavity and hence with the artificial burrow.

One of the salamanders in container C (with tubes) survived for 40 days (Table I). The other desiccated at an earlier undetermined date. After the first day, the former remained below the surface of the sand continually, finally desiccating in the tube. The latter persisted in following the edge of the container and did not encounter a tube until the 7th day, when I placed it in front of the mouth of a tube. It immediately entered and stayed there for most of the remainder of the experiment. The 2 salamanders in container D (lacking artificial burrows) were unable to burrow and consequently desiccated in only 26 and 34 days respectively. In container C the moisture content of the top centimeter of sand decreased from 26.6% dry weight to 0.3% during the experimental period. Moisture content fell from 26.6 to 3.3% in the surface centimeter in container D and to 4.4% in the 2nd centimeter. Measurements of soil moisture were made at the time of desiccation of the salamanders and, as death occurred much sooner in container D, it had a higher final moisture content than C.

Some ability to burrow in humus and leaf-fragments bound with rootlets, was exhibited. Both salamanders in container D (fragments with root-

TABLE I. Comparison of survival time and first occurrence of coiling and burrowing by *Plethodon cinereus* during drying of various substrates in Experiment 2. Data for C are incomplete because the salamanders could not be observed while underground. In container C the substrate was allowed to dry to the bottom. A moisture gradient was present in the rest of the containers at the end of the experiment. Container C had artificial plastic tubes and subterranean cavities; D, E, and F lacked tubes and cavities

Snout-anus length (mm.)	Color type	Container no.	Substrate	Water content of substrate at saturation (ml water per ml substrate)	DAYS FROM BEGINNING OF EXPERIMENT TO: First coiling	First burrowing	Death
26	red	C	Sand	0.25	—	—	—
36	red	C	Sand	0.25	—	—	40
29	black	D	Sand	0.25	did not coil	did not burrow	26
24	red	D	Sand	0.25	28	did not burrow	34
25	black	E	Leaf-fragments and rootlets	0.15	15	4	23
35	red	E	Leaf-fragments and rootlets	0.15	15	6	22
29	red	F	Humus	0.41	14	28	35
33	red	F	Humus	0.41	33	did not burrow	42

lets) penetrated to a depth of 1 cm below the surface of the substrate in 2 separate locations. One burrow was made between the fragments and the glass wall of the terrarium where rootlets did not have a binding effect; the other was excavated 2 cm from the nearest wall. In each, a cavity just large enough to contain the salamanders was formed, presumably through body movements. Sometimes both individuals occupied the same cavity, although they shifted their location from one cavity to the other. At first they remained in the burrows with their heads facing outwards just below the surface of the substrate. This was also a very frequent position in the plastic tubes and agrees with similar observations by Test (*op. cit.*). As drying continued, they withdrew completely below the surface.

Although these salamanders were able to make their way through the leaf-fragments bound with rootlets, their progress was slow and they desiccated before reaching sufficient moisture to keep them alive. At the conclusion of the experiment, there was still a moisture gradient present in the fragments. The moisture content of the surface centimeter of fragments was 34.6% of dry weight, the next deepest centimeter 127.8%, the 3rd 151.5% and the bottom 3 cm taken together 186.1%. At the beginning of the experiment, moisture content was 393.0%.

The evidence from container G confirms the above results. After all of the salamanders in the other cages were dead, it was excavated to ascertain the salamanders' positions. The fragments had desiccated from 393.0% to 15.6% of dry weight and the salamanders were dead. One had penetrated the fragments laterally to a distance of 1.5 cm; the other had made a tunnel 3.0 cm long between the fragment layer and the bottom of the container but was in its original cavity when death occurred.

Displaying even less competence for burrowing in humus than in fragments bound with rootlets, one individual (the larger) in container F did not burrow at all. The smaller one succeeded in working its way partly under a rootlet protruding from the substratum. During the experiment, the humus had gone from a moisture content of 336.0% to 56.7% of dry weight in the surface centimeter and to 116.6% in the second centimeter.

In experiment 3, observations were made on the terrarium containing sand 42 times, and on every occasion all 6 salamanders were either on the sand or climbing on the glass. None was able to enlarge a small hole enough to occupy it. An attempt had apparently been made to enter at least 5 of the small holes, for the upper 3 mm had been enlarged from 2.5 mm in diameter to 6 mm x 4 mm. The head width of the salamanders used in the experiment ranged from 4 mm to 6.5 mm.

Holes in humus were easily enlarged. The morning following initiation of the experiment, one of the salamanders was in a hole with only its head protruding. That evening it was at the same location and 3 other holes had been enlarged although none of the latter were occupied at that time. By the evening of the 2nd day, only one salamander was still above the surface of the humus. It was observed attempting to enter one of the holes, but it quickly backed out as though the tunnel were occupied.

On July 4, 1958, five days after beginning the experiment, all salamanders were removed from the humus and its original condition restored. For the remainder of the experiment only 4 salamanders were used. On July 5, one had enlarged a hole and was occupying it. By July 10, four holes had been enlarged and 2 new ones formed in a crack which had resulted from drying of the substrate's surface. The position of salamanders noted in the previous experiments (in a tunnel with the head at the opening and facing out), was again common. Also, on 3 occasions salamanders were seen in the tunnels with only the end of the tail protruding. At the end of the experiment, although all tunnels were still vertical and none of the salamanders had made lateral extensions in them, they had been enlarged sufficiently to allow the salamanders to turn around. It seems very unlikely that any of the animals backed into the holes. The final diameter of the largest opening to a tunnel was 8.5 mm although greater diameters were encountered beneath the surface.

On July 1, I intermittently watched one of the salamanders on humus enlarging a previously unmolested hole. Its snout was inserted into the hole. The neck was curved and the head forced downward by pushing with the forefeet. Lateral head movements were employed at the same time. Frequently the salamander lifted its head briefly and then renewed its efforts. Occasionally it left the hole, later returning to it. When the hole was enlarged enough that the forelimbs could be inserted, the rear feet served to push the animal into the hole, again by a force exerted backward on the humus. Often the feet would slip on the substrate. At this stage, the forelimbs may have aided in burrowing although they could not be seen. In the later stages when the rear feet were near the hole, the tail was bent into an arc with the distal one-third of it appearing to exert force against the humus. The process lasted from noon until 5:30 P.M., although the salamander was not continuously engaged in burrowing.

Evidently, the burrowing of *P. cinereus* cannot be called digging in any sense of the word. Rather the animal uses its head as a wedge and forces its body into cracks or small openings in the substrate by pushing with its feet, and in some instances, its tail. With such a method of burrowing it is easily understandable why this species is inefficient in penetrating sand or smooth surfaces. Under natural conditions, where many irregularities exist in the surfaces of all the layers of the forest floor, humus is probably not an effective barrier to vertical migration. However, sand is quite impenetrable unless holes originating from sources other than salamanders are present.

For the sake of behavioral analysis the time span of experiment 1 can be divided into 5 periods, I through IV containing 5 days each and V with 3 days. The number of observations per container were 30, 42, 26, 22, and 12 for these periods, respectively. Since observations were made less frequently in experiment 2, there were 4 periods (I-IV), each containing 10 days, except the last one which varied from 2 to 12 days depending on the time of death of the salamanders. If only a few observations were available for an end period, they were grouped with the preceding one. Numbers of observations per container per period ranged from 19 to 52.

Figure 2 shows the location of the animals during experiment 1. It is readily seen that as the substrate dried, the percentage of observations in which salamanders were on the exposed sand decreased, whereas those in which the animals sought cover increased. By period III the salamanders in container B (without tubes) remained a large proportion of the time under the bark where conditions were least dry. In container A which contained several shelter sources (bark, tubes, and cavities under the sand), as progressive drying occurred, the less favorable sites were abandoned for those deeper underground. By the end of the experiment the salamanders were in the cavities the majority of the time. Their tendency to follow the plastic burrows beneath the ground in container C has already been mentioned. Unfortunately, at the time when salamanders were inhabiting the plastic tubes it could not be discerned whether condensed water was present on the tube walls or not.

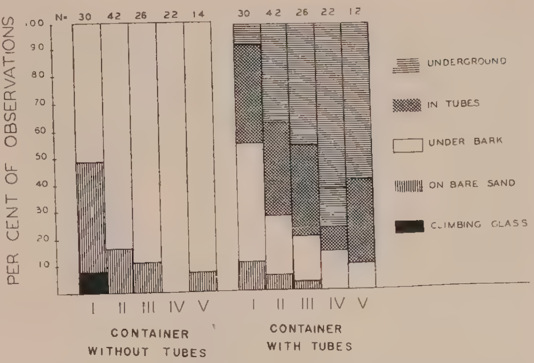

FIG. 2. Locations of salamanders during drying of substrate in experiment 1. I-IV are successive periods of 5 days each. V is a period of 3 days.

During experiment 2 the substrate in one half of container D dried more quickly than that in the other, as evidenced by a color difference of the sand. The records of salamander locations were analyzed excluding 11 observations in which they were climbing on the walls of the container. Salamanders were on the faster drying side only 14 times out of 84 (highly significant when tested by chi-square). The times when salamanders were on the drier side were, with two exceptions, within the first 10 days of the experiment when conditions were wettest. Thus, the salamanders inhabited the moister side almost exclusively when water became a critical factor. The other containers did not exhibit visible differential drying and salamanders were more uniformly distributed.

In addition to the seeking of more favorable sites, other behavioral responses to desiccation occurred. When first placed in the experimental situation, *i.e.*, when moisture conditions were still favorable, the salamanders' activity consisted chiefly of climbing the sides of the glass container or moving about on top of the substrate. Each individual was found in a different location almost every time observations were made. Later, conservation of moisture apparently played a dominant role in influencing behavior and, as conditions became drier, the salamanders tended to remain in the same location, in one instance for as long as 11 days. They abandoned their former position of lying stretched out and adopted a coiled position, thereby decreasing the area from which evaporation could occur. The exact position varied from a circular coil to a tight S-shaped one. In experiment 1, incidence of coiling increased from less than 5% near the beginning to over 90% at the end (Figure 3). In experiment 2, incidence of coiling increased on all 3 substrates (Figure 4) and by the end of the experiment reached over 30% on sand, almost 90% on leaf-fragments and slightly over 50% on humus. In 2 different containers, aggregations of coiled individuals occurred. It is probable that these were formed simply because each salamander oriented itself to the most moist object in its environment, which happened to be the body of another salamander.

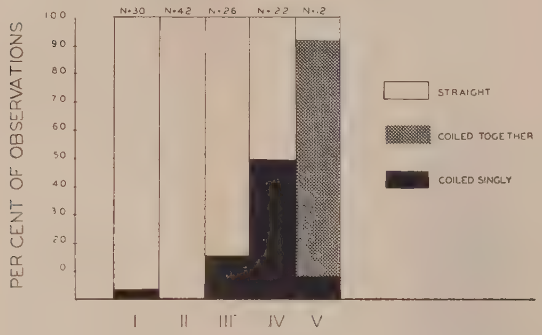

Fig. 3. Position of salamanders on sand in container without tubes, experiment 1. I-IV are successive periods of 5 days each. V is a period of 3 days.

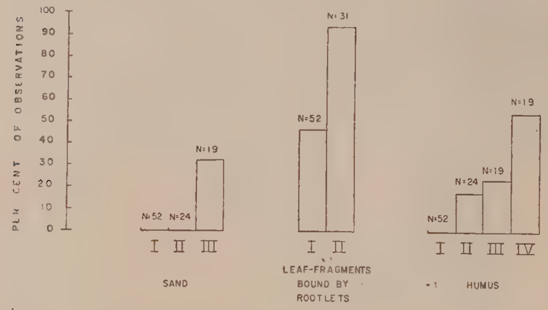

Fig. 4. Percentage of observations in which salamanders were coiled. Experiment 2. I-IV are successive periods of 10 days each except for a variable amount of time in the terminal ones.

An important response by the salamanders, not brought out in the figures because of its short duration, was a final burst of activity. After the inactive period and less than one-half day before death, individuals left shelter and wandered about, apparently at random, until disabled. Dead animals were usually found on the surface of the substrate.

Discussion

Burrowing by plethodontids has been the subject of some controversy in the literature. Noble (1927) inferred that *Plethodon* follows crannies into the ground, to which Dunn (1928) replied that, "any one who has ever kept salamanders in terraria knows full well that even such non-elongate forms as *Desmognathus* and *Plethodon* make their own burrows and do not merely 'follow crannies'." I kept 17 individuals of *P. cinereus* for 6 months in a terrarium containing leaf litter and leaf-fragments which were not bound together by rootlets. The salamanders moved about freely in the material and distinct tunnels or burrows were formed. Also, members of this species have been observed to disappear rather quickly in humus which had been freshly disturbed and loosened by mechanical means. Vernberg (1953) stated that individuals of *P. cinereus* burrowed in beakers filled with a silty loam, although the degree of loosening the soil underwent in being removed from its natural site was not indicated. In the field he also demonstrated vertical movement through sandy loam. Whether this represented actual burrowing or simply passage through already existing tunnels and crevices was not important for the purpose of his study and apparently was not determined. *P. cinereus* can penetrate the upper layers of the forest floor whereas the deeper, more compact ones, or those which are matted together by a network of closely intertwining rootlets, serve as a partial barrier. The soil may be either a partial or complete barrier depending on the type involved.

Plethodon jordani can burrow in soil, at least to some extent. Brooks (1946) watched individuals of this species emerging from a bank and witnessed some of them make the openings through which they came." On the basis of field and laboratory observations on *Plethodon metcalfi,* Chadwick (1940) expressed the opinion that this salamander does not make its own burrows but may extend and improve them. *Plethodon jordani melaventris* makes digging motions against the floor of an experimental chamber when undergoing desiccation (Gordon 1952). Thus the opposing views of Dunn and Noble may have arisen because they were dealing with different substrates or perhaps different species of *Plethodon.*

Penetration of some of the more compact material by *P. cinereus* is facilitated by the presence of solid objects as evidenced by the fact that the only successful burrowing in container F occurred when a salamander worked its way under a protruding rootlet. Also, one of the excavations in container E was between the container wall and the substrate. This is quite easily understood when the method of burrowing is considered. A solid object, in addition to breaking the continuity of the substrate, provides a firm surface against which a salamander can apply the force necessary to push its head forward.

The partial dependency of *P. cinereus* upon earthworms, insects and other burrowing forms for providing a means of penetrating deeper, moister layers during dry periods is evident. Plants also may be quite important, for decayed roots leave channels in the soil and solid roots may provide a surface along which the salamanders can work their way into the substrate. However, high densities of herbaceous plants or seedlings resulting in a heavy, impenetrable mat of rootlets has an adverse effect.

The direct influence of *P. cinereus* on its physical environment must be very slight except perhaps through its activities in the litter and fragment layers and in keeping burrows previously made by other animals open.

Coiling behavior of *P. cinereus* when subjected to dry air was previously noted by Shelford (1913). Cohen (1952) studied behavioral responses to dehydration in *Aneides lugubris* and *Ensatina eschscholtzii xanthoptica*. The former exhibited coiling and desiccated slower than the latter which lacked this behavior. However, coiling is not to be considered a characteristic feature of the family Plethodontidae. In a study of 8 species, 7 of which were plethodontids, Ray (1958) found that 3 species (*Batrachoseps attenuatus, Aneides lugubris,* and *A. ferreus*) coiled when desiccated, whereas 4 did not (*Ensatina eschscholtzii, Aneides flavipunctatus, Plethodon elongatus* and *P. dunni*). The former species occur in habitats subject to periods of drying, whereas the environments of the latter 4 are usually more moist. It can be seen that this behavior pattern is not constant even within a genus (Compare *A. lugubris* with *A. flavipunctatus* and *P. dunni* with *P. cinereus*) but appears to be a specialization of certain species which encounter unfavorably dry conditions.

Behavior patterns may be placed into an order of occurrence by referring to Figures 3 and 4 and Table I. As *P. cinereus* loses water, it first moves to a more favorable site. Next, if the substrate is favorable, it burrows. Still later the salamanders coil. Sometimes the latter 2 behavior patterns are in reverse order; coiling may be followed by burrowing activity, or may occur within a cavity which has already been formed by the animal. Presumably, coiling in burrows indicates inability to penetrate the substrate farther to reach favorable conditions. Finally, wandering preceding death occurs, and in the natural habitat may lead to finding moist conditions.

In the experimental containers, death occurred rapidly on fragments (22-23 days), more slowly on sand (26-34 days when artificial burrows were not supplied), and slowest on humus (35-42 days). Since, at saturation, humus contained over one-third more water per unit volume than sand, and almost 3 times as much as leaf-fragments (Table I), survival time appears to be related to initial moisture content of the substrate. The highest incidence of coiling occurred on leaf-fragments (Figure 4). Survival time cannot be compared between experiments 1 and 2 as they were not carried out concurrently and the presence of pieces of bark in the former contributed a variable not found in the latter. Survival time in G was undetermined because of the nature of the experiment.

SUMMARY

Plethodon cinereus is unable to burrow in sand from its natural habitat, but can burrow in humus if solid objects are present or if the humus has been loosened mechanically. Burrowing does not occur in undisturbed humus.

This species can burrow in fragmented leaves (F layer) unless large numbers of rootlets are present which bind the leaf-fragments together. Small holes already present in humus are easily enlarged but the salamanders are unable to enlarge those in sand.

In sequence of occurrence, the behavioral responses to desiccation by *P. cinereus* are (1) movement to more favorable sites, (2) burrowing if substrate is favorable, (3) coiling, and (4) wandering.

Burrowing is accomplished by using the head as a wedge, the feet and tail supplying the force necessary to push the head into the substrate or between objects.

Relative survival time on different substrates correlates with the water-holding capacity of the substrates. Death ensues rapidly on leaf-fragments, more slowly on sand, and still more slowly on humus.

ACKNOWLEDGMENTS

I would like to acknowledge the invaluable aid afforded by the criticism and suggestions of Professor Frederick H. Test of the Zoology Department, University of Michigan. Drs. Charles F. Walker, William R. Murchie, and Stephen H. Spurr, all of the University of Michigan read the manuscript and offered comments. Professor Alfred H. Stockard is gratefully acknowledged for making the facilities of The University of Michigan Biological Station available. My wife, Audry Heatwole, prepared the figures. The research was carried out during tenure of a National Science predoctoral fellowship.

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BEHAVIORAL ECOLOGY OF THE CRAB, *PACHYGRAPSUS CRASSIPES*

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I. Aggressive Behavior and Spacing

In *Pachygrapsus crassipes* Randall, a Pacific shore crab, two behavioral features stand out. It is an amphibious species occupying both pools and the surrounding rocky shore, with the adults ranging high above the surf, and it is a particularly aggressive species. The relationship of this local dispersion pattern to the aggressive behavior is central to this report on a series of experiments done at the Hopkins Marine Station, Pacific Grove, California.

Field notes

A patient observer in a frozen posture may record activity without disturbing the animals. Observations important to the concepts to be developed should be noted; they corroborate the findings of Hiatt (1948) in his monograph on the species.

P. crassipes is characteristically a rocky intertidal form though dense populations may be found in tunneled estuarine mud banks. Basically aquatic in terms of gaseous exchange, feeding and breeding, they may remain in moist crevices for hours. Individuals were seen to descend into a pool, immerse, and retreat to the same higher point. Hewatt (1937) lists the intertidal range from mean low water to plus 5 feet; Hiatt (1948) to plus 8 feet. Juveniles appeared to be more closely tied to the water and adjacent rock crevices.

Field observations and stomach analyses indicate omnivorous food habits. They were seen to attack and eat other crabs and living cottid fish, and also to scavenge and graze on algae; one stomach was entirely filled with shredded *Ulva* fragments. Hiatt (1948), emphasizes their herbivorous nature; Pearse (1931), while noting the algal feeding, cites the truly hunting behavior; Ricketts and Calvin (1948) name the species as the most active scavenger of the tide pool.

While clearly omnivorous, the predaceous nature of the animal is pertinent to the thesis; whatever the food, feeding is largely done in the pools and during darkness.

Large numbers of adults occupy deep rocky fissures well above the water, particularly during daylight. They display very little aggressive behavior and tend to aggregate, several crabs to a crevice. They are very inactive in these retreats unless disturbed, upon which they withdraw farther and assume the rearing defense posture.

In the tidepools, very different behavior is displayed. Here they tend to occupy underwater fissures but actively forage even during daylight hours. There is no aggregation; no more than one crab per crack is allowed and tension contacts commence at any close meeting. The crevice occupied at the moment is defended but even semipermanent residence in one particular site is not apparent. Density appears to be related to the number of habitable irregularities in the rocky sides of the pool. The larger crabs are dominant over the smaller and the males more aggressive than the females. As in crayfish (Bovbjerg 1953, Lowe 1956), various levels of aggression were displayed; these are categorized as avoidance, threat, strike, and fight. The latter may result in an eviction from the crevice occupied. Unlike crayfish, whose sensory organs in this respect are the antennae (Bovbjerg 1956), the tactile organs of crabs are the walking legs; locomotion is lateral with very delicate probing movements of the individual walking legs.

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[1] These investigations were done as visiting professor in marine ecology at the Hopkins Marine Station of Stanford University.

Experimental procedure

To clarify the nature of the aggressive habits and the effect of the presence and absence of water in the environment, small groups of crabs were established in laboratory bowls and observed in the presence and absence of water during alternating periods. Polyethylene bowls of 30 cm diameter were covered with screen and surrounded by drapes with viewing slits. The bottom was covered with beach sand; the water was 8 cm deep and changed daily. Algal food (*Ulva* and *cladophora*) was maintained. Two cast concrete blocks formed a crevice 5 cm deep (Figure 1). Four crabs comprised a group with adequate space for foraging, occupying the crevice or climbing onto the concrete blocks. Since the single desirable crevice was small, tension contacts were assured.

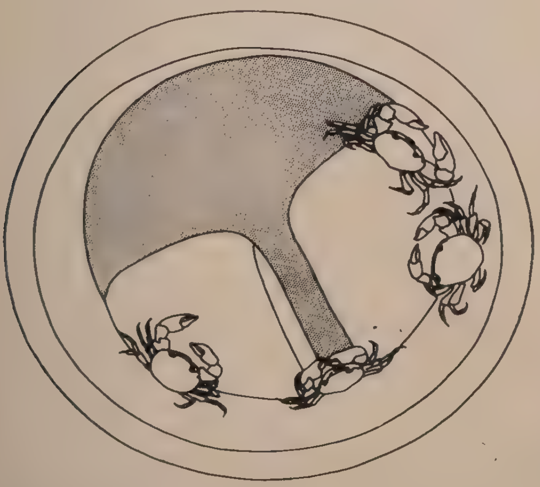

FIG. 1. Experimental group in water filled bowl. (from photograph)

The animals taken from the field, were all healthy, hard, adults with intact appendages; they were identified with laquer markings. Each group was observed for one hour daily over 5 day periods, the periods with water alternating with water drained. Fourteen groups were studied, 4 of males, 4 of females, and 6 of mixed sex groups. The recording procedure used was that described for crayfish (Bovbjerg 1953).

At infrequent intervals (of no less than one-half hour) recordings were made of each crab's position. Data were secured during periods with water present and periods with water absent.

Results

In 112 periods of observation, 856 tension contacts were recorded. When reduced to contacts per hour, the data for different groups and conditions become comparable; these are summarized in Table I.

TABLE I. Summary of data on tension contacts of 14 groups of 4 crabs in bowls with water and with water drained

		IN WATER			OUT OF WATER		
No. of Expts.	Sex	Tension Contacts	Observ. Periods	Tens. Cont. hour	Tension Contacts	Observ. Periods	Tens. Cont. hour
4	female	178	23	15.5	25	10	5.0
4	male	313	23	27.2	22	8	5.5
6	mixed	310	28	22.1	8	20	0.8
T=14		T=801	T=74	M=21.7	T=55	T=38	M=2.9

Tension contacts of groups in water filled bowls were 7 times those of groups in drained bowls. Male groups had twice as many tension contacts as female groups; in mixed sex groups, all males were dominant to females, in many instances over larger females, although it was difficult to distinguish aggressive behavior from the onset of a complex sexual ritual described elsewhere (Bovbjerg 1960). Within most of the groups there was a size difference between individuals of 5 mm or less in carapace width. Nevertheless, size was directly related to dominance. Between closely matched individuals of the same sex a millimeter or 2 difference in size was enough of a cue to establish subservient reactions on the part of the smaller.

Definite straight line hierarchies of dominance were established in 11 of the 14 groups.

In laboratory bowls where no escape is possible, fights may result in casualities. Autotomy of legs during combat was frequent and molting inevitably led to cannibalism. On one occasion, a hard-shelled crab was killed during a fight; it was crushed in mid-carapace and the viscera spooned out by the free chela of the aggressor. Such an event would be far less likely in nature; it was not observed by Hiatt (1948) in his extensive observations.

Of the more than 400 position recordings, 85% were on or between the concerte blocks rather than on the sand, a rather obvious corroboration of an obvious substratum preference. Of more importance, aggregation of all 4 crabs in a group occurred only 6% of the time in water filled bowls and 43% in drained bowls. Amicable contact between one or more crabs was demonstrated in 75% of the recordings in drained bowls while in only 30% of these in water filled bowls. These data are in agreement with the dominance studies; aggregation and lack of tension contacts were more characteristic of groups of crabs out of water; while spacing as a function of tension contacts is an attribute of groups in water.

Juvenile crabs exhibit the same types of aggressive behavior with some modification. Dominance relations are established and spacing is prominent. The movements are more rapid than those of adults and threats and strikes are more often employed than fights. The threatening and chasing, among themselves as well as inanimate objects such as scraps of algae, bear a startling resemblance to the play activities of young carnivorous mammals.

Interpretation

An instinctive and precocious battery of aggressive reactions is prominent in *P. crassipes;* in laboratory bowls social hierarchies are formed. The species thus joins the ranks of crustaceans for which such behavior has been reported: the crayfish, *Orconectes virilis, Cambarus alleni* Bovbjerg 1953, 1956), *Cambarellus shufeldtii* (Lowe 1956), the lobster *Homarus americanus,* the crabs, *Pagurus longicarpus, P. polycarpus, Callinectes sapidus,* and *Libinia emarginata* (Allee and Douglis 1945, Douglis 1946).

In nature such hierarchies would not develop; aggressive behavior would lead to spacing and thereby to regulation of a density far lower than that in laboratory bowls. This phenomenon is surely not characteristic of all decaped crustaceans, for instance, the pelagic forms. Nor is it present in all littoral species. *Petrolishes cinctipes,* a small filter-feeding crab, is such an exception. On the California coast it is common under stones and in the base of *Mytilus* beds; here they are in obvious aggregation. Several groups were observed in the laboratory over a period of weeks; aggregation was the rule and no tension contacts were noted.

The superimposition of the terrestrial capacity upon the primary marine nature of *P. crassipes* may have resulted in the behavioral differences in and out of water. The feeding and breeding aspects are aquatic and related to aggressive behavior. Conversely, the occupation of supra-tidal rock crevices is related to defensive rather than aggressive behavior. This suggests an evolutionary escape from marine predation with survival value in the aggregation of crabs in the relatively few suitable crevices out of water. The conservation of water by aggregated crabs in such a situation may be of importance.

II. DISPERSAL OF EXPERIMENTAL POPULATIONS RELATED TO DENSITY

P. crassipes manifests strong aggressive and spacing behavior. It has been postulated that such an animal would tend to disperse in a density related fashion as do crayfish (Bovbjerg 1959). To test this hypothesis, dispersal experiments were done. Field experiments proved technically impossible in the complex physical and biotic environment of the rocky shore habitat. Therefore a simulated tide pool was constructed in an outdoor tank where the dispersal rates of various sized groups of crabs could be measured.

Experimental procedure

A small brick pool was constructed within a larger screened tank of 1 by 2 meters. (Figure 2). A partition in the center created a U shaped pool, essentially 2 crevices and a small open area. The bottom of the entire tank was sand-covered and fresh sea water was maintained at a 10 cm depth. Algal food was replenished throughout.

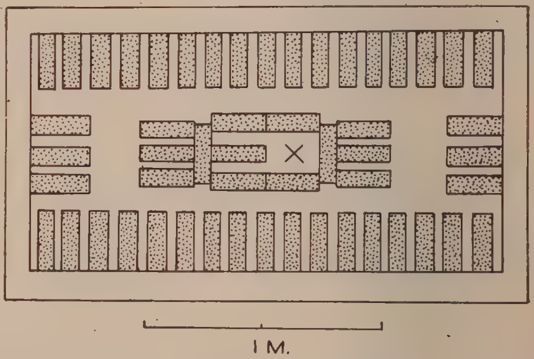

FIG. 2. Plan of experimental pool within 1 x 2 m concrete tank. Stippled rectangles represent bricks; X is point of release within inner pool.

The tank was lined with spaced bricks to create an excess of crevices. The 2 habitats were similar but for size and number of hiding places for crabs; theoretically, the inner pool could contain 3 individuals without threatening contact while the larger pool could accommodate a very large number.

A stock of about 30 crabs was maintained in the tank; small increments were regularly added and returned to the sea to ensure a turnover while allowing time for acclimatization. The animals were intact, healthy adults of both sexes.

Groups of 5, 10, 15, and 20 crabs were released in the inner pool and the number of residents *vs.* the number of emigrants was recorded after a 2-hour period. Thirty trials were made at each density, a total of 120 experiments. The hypothesis was that the simulated tide pool could accommodate only 3 crabs regardless of initial density and that the remainder would emigrate by crawling out into the larger pool.

Results

The number of residents *vs.* emigrants for each size group is recorded in the histogram of Figure 3. In the 120 trials of all groups, the mean number of residents was 3.4 crabs; the mode (¼ of the trials) was 3 crabs. In 4 instances, all of the crabs emigrated; only once were there more than 7 residents. For the 5 crab group the mean resident number was 2.7 ± .48, for 10 crabs: 3.0 ± .46, for 15 crabs: 3.6 ± .67, and for the 20 crab group: 4.3 ± .67. Regardless of initial density, the final number of residents approached the theoretical number of 3. The greater the initial density, the greater was the rate of emigration.

Subjective observation corroborated this density-dispersal relationship. The amount of tension contact varied directly with density; at 20 crabs per pool, an immediate melee resulted in prompt emigration—large numbers boiling out over the edge of the pool. At the 5 crab density there were pair tension contacts but emigration was sporadic.

Twelve of the 20 density groups were observed over the entire 2-hour period. Figure 4 records the rates of dispersal for these groups. Very clearly, the rate is highest in the first 20 minutes, tapering markedly in the last hour. The slope of the curve at 2 hours is still declining, suggesting that the mean of 4.3 is not yet optimal for 20 crab groups in this pool. The validity of the mean curve is enhanced by the correspondent curves of the extremes. Though varying somewhat, the slopes of the 12 individual curves were very similar. This change in rate of dispersal of groups of 20 crabs bears a striking resemblance to that similar crayfish groups (Bovbjerg 1959).

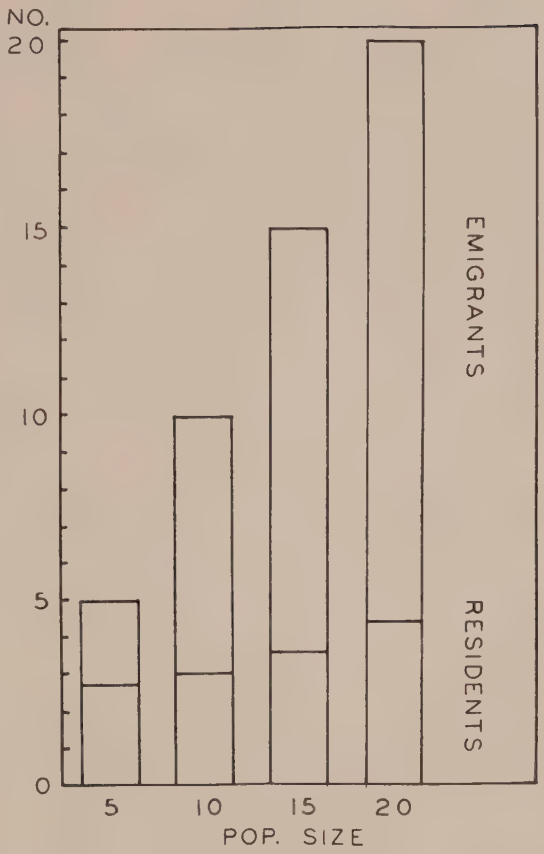

FIG. 3. Mean numbers of residents and emigrants for each population size.

Interpretation

Since the aggressive behavior of *P. crassipes* results in spacing, the number of suitable crevices and the size of the pool would seem to determine population size. Overpopulation could be alleviated by emigration out of the water. Therefore, behavior is directly related to the local dispersion pattern and ultimately to density within the larger shore habitat. The experimental data confirm field observations in support of this proposition. This density related concept of dispersal is in opposition to that of Andrewartha and Birch (1954) who describe dispersal as an inherent tendency unrelated to density.

The behavioral ecology of *P. crassipes* seems related to their broader ecology in 2 ways. First, this may be the most important device regulating

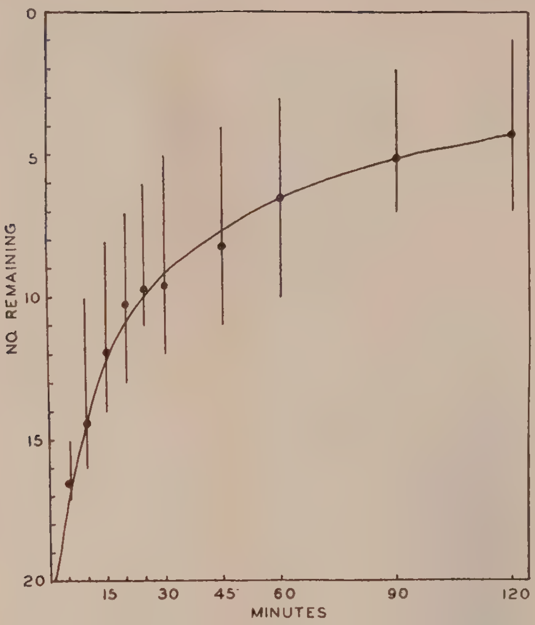

FIG. 4. Mean rate of dispersal of 12 groups of 20 crabs over the 2-hour period.

local density and hence related to population well-being in terms of food and space needs. Second, emigration from an overpopulated pool is insurance that all optimal portions of the larger habitat are occupied or are reoccupied after local decimation.

SUMMARY

1. Field data on an amphibious crab, *Pachygrapsus crassipes* Randall, indicate strong aggressive and spacing tendencies in tide pool populations.
2. Laboratory observations confirmed these data as to the high level of aggression. But a marked difference in behavior was noted when crabs were in or were out of water. Under the latter conditions, aggressiveness is diminished and replaced by a tendency to aggregate.
3. Further experiments were done in a simulated tide pool within a larger tank. Groups of 5, 10, 15, and 20 crabs were released and emigration *vs.* residence recorded after 2-hour periods.
4. Dispersal appears to be related directly to initial density, the amount of emigration being greater in the larger groups.

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ENERGY FLOW OF A SALT MARSH GRASSHOPPER POPULATION[1]

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Analysis of communities by measuring the energy transformations of constituent populations is largely untried. Some energy flow measurements of whole ecosystems have been successfully undertaken (Odum 1957, Teal 1957) and a laboratory population has been the subject of some excellent work (Richman 1958). The present paper describes a study of the energy flow of a natural population of a grasshopper, *Orchelimum fidicinium* Rehn and Hebard, in salt marshes near Sapelo Island, Georgia.

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[1] Contribution No. 24 from the University of Georgia Marine Institute. This research was supported by funds from the National Science Foundation.

Organisms in nature may be looked upon as systems which accumulate energy in the form of protoplasm. The accumulation of energy by organisms is what we commonly call production. Since organisms must overcome the tendency for energy to disperse, or assume a more random form, work is required for production, as well as for reproduction and maintenance of life. This work is directly proportional to the respiration of an animal. The energy which an animal acquires from its food will largely appear either as production or respiration; the sum of these processes is called energy flow and is approximately equal to assimilation through the wall of the gut, at least in higher animals. Energy flow will more accurately represent the significance of a species in a community than either the numbers or biomass of that species (Odum and Smalley 1959).

Orchelimum fidicinium is an abundant and conspicuous insect in Georgia salt marshes. The nymphs first appear in late April and early May, and by the middle of August only scattered individuals remain. One generation is produced each year, and hatching occurs within a short period of time. A population which hatches, grows and dies within one year presents some excellent advantages for the study of population energy flow in nature. *Orchelimum* is most common in moderately tall, dense *Spartina alterniflora* Loisel. They are not found in extremes of *Spartina* growth, in the very tall grass (over 2 meters) along the larger creeks, nor the very short grass (under one meter) growing in extensive areas of high altitude, poorly drained marsh. During high tides the grasshoppers cling to *Spartina* stems which project above the water. They will dive under water readily at the approach of man or boat, but normally they are entirely aerial. During very high tides, grasshoppers are vulnerable to predators, as has been confirmed by observations in the marsh; however, unusually high mortality during spring tides has not been detected by quantitative sampling. *O. fidicinium* is the only species of grasshopper commonly found on the open marsh, although other species occur in proximity to terrestrial vegetation.

METHODS

The grasshoppers were sampled with a sweep net every 4 to 6 days during the spring and summer of 1957. Five samples of 25 uniform sweeps each were taken, all by the same person. Successive samples were not taken in the same place because of the possibility of depleting the population. Similar areas were chosen for the samples on the basis of marsh altitude and *Spartina* height and density, but the samples were not random. Since no systematic relationship between the appearance of the marsh and the density of the *Orchelimum* population could be discerned, this procedure had an element of randomness, as long as efforts were confined to the same general marsh type.

The samples were taken to the laboratory, the grasshoppers killed and counted, and the total length of individuals and the dry weight of each size class recorded. Oven dry weights were used throughout. Nymphs were classified into 4 arbitrary size classes differing by 5 mm intervals. Adults were not sorted into size classes.

To convert the results of the sweep samples to numbers per unit area, a modification of the method used by Beall (1935) and Cross (1957) was adopted. A cage was constructed which was one meter square and 75 cm high, and covered on the sides and top with fine mesh copper screening. The cage was held between 2 men, who then ran over the marsh, and at a signal, placed the cage sharply down on the ground. The grasshoppers were picked out, counted and released. The cage samples were then compared with sweep samples taken on the following day and the resulting ratio used for converting sweep samples to grasshoppers per unit area.

Oxygen consumption rates of grasshoppers of different sizes were determined in a variable volume respirometer consisting of a pipette inserted into a stoppered vial. The animals were placed in the vial along with a CO_2 absorbent and the apparatus immersed in a constant temperature water bath. The progress of the water into the free end of the pipette measured the amount of oxygen used by the animals. Provision was made for re-injecting air into the system at intervals, although all of the experiments were of short duration so that the animals would not be in an oxygen poor atmosphere. Oxygen was plotted as ml 0_2 consumed /hr/ animal against weight of individual animals. Since there was a linear relationship between the log of the weight and the log of the oxygen consumption, the regression of oxygen consumption (Y) against weight (X) is given according to the equation

$$Y = aX^b$$

where a and b are constants, as suggested by Brody (1945) and Bertalanffy (1957). Oxygen consumption was also measured over the range of temperatures occurring on Sapelo Island during the summer of 1957, and the regression of oxygen consumption on temperature was calculated. In converting oxygen consumed to calories produced as heat, the grasshoppers were assumed to have fed exclusively upon *Spartina alterniflora*, the only higher plant found on the marshes where the grasshoppers were studied. In addition, it was assumed that cellulose was not assimilated by the animals. Burkholder (1956) gives an analysis for *Spartina*. The caloric yield, per milligram of oxygen consumed, for fat, protein, and N-free extract was obtained from Ivlev (1934). From these data, a mean caloric yield of 4.93 cal/ml O_2 was calculated, and used to convert O_2 consumption of the grasshoppers into calories. The caloric content of *Orchelimum* and *Spartina* was determined by combustion in a Parr Adiabatic Bomb Calorimeter.

To determine defecation rates, grasshoppers were kept in a container with *Spartina* leaves for short periods (from 2.0 — 2.7 hrs.) immediately after being collected from the marsh. Both feces and grasshoppers were dried at 100°C and weighed, and the respiration of the grasshoppers at the experimental temperature was calculated from the previously described regression. The rates of production, assimilation and defecation were assumed to have been in the same ratios throughout the population, even though production was low or absent in adult grasshoppers. The sum of defecation, production and respiration provides an estimate of the rate of ingestion.

RESULTS

The results of the cage-sweep sampling, and the resulting conversion coefficients of 0.79 m^2/sweep for nymphs and 1.66 m^2/sweep sample for adults, are shown in Table I. Adults are apparently captured more efficiently by sweeping than are nymphs because the adults fly away near grass-top level and are caught by the net, while nymphs hop down into the lush growth of *Spartina* and evade the sweep net. Cross (1956) found that sweeping was more efficient for nymphs than adults of *Melanoplus* in old fields, but the vegetation in these fields was typically of much lower density than in the *Spartina* marsh.

TABLE I. Estimates with a portable cage of the number of grasshoppers captured with a sweep net. For the cage samples, N = 12; for the sweep samples, N = 10

Date	GRASSHOPPERS/SAMPLE				SQUARE METERS/ SWEEP SAMPLE	
	Cage samples		Sweep samples			
	Nymph	Adult	Nymph	Adult	Nymph	Adult
July 22-23, 1957......	2.00	3.17	2.20	12.80	1.10	4.04
Aug. 11-12, 1957.....	0.50	1.50	0.60	2.90	1.20	1.93
July 1-2, 1958........	8.50	4.50	6.60	5.10	0.78	1.13
July 8-9, 1958........	3.75	3.83	2.30	3.00	0.61	0.78
July 10-11, 1958......	1.67	2.92	1.10	5.60	0.66	1.92
July 10-11, 1958......	2.50	4.50	2.20	4.50	0.88	1.00
Mean	3.15	3.40	2.50	5.65	0.79	1.66

Table II shows the results of the periodic sampling and the mean weights of the individual animals in each size class. There is no ready explanation for the abrupt decline in population which occurred from May 18 to May 22 and from June 19 to June 26. Examination of tide records during these periods failed to show any correlation between grasshopper mortality and tide height. The census figures in Table II were converted to grasshoppers/m^2 on the basis of the cage-sweep ratios and plotted as the log of population density against time (Figure 1). The population density on June 19 is the mean of 2 samples. The average mortality, or number of individuals dying, was calculated from the regression of Fig. 1 by taking the difference between the number of grasshoppers at the beginning and at the end of each sampling period. The mortality rate was assumed to be the same for each size class. Since all of the grasshoppers die during the summer, the total biomass lost by mortality was used as an estimate of population production. Egg production was not accounted for, except to

TABLE II. Numbers (N) and dry weight in grams (W), of *Orchelimum* taken in 5 sweep samples of 25 sweeps each, or adjusted to this sample size

	0-5 mm		5-10 mm		10-15 mm		15-20 mm		Adult		Total	
	N	W	N	W	N	W	N	W	N	W	N	W
May 13......	146	0.41	68	0.48	—	—	—	—	—	—	214	0.89
May 18......	110	0.44	144	1.59	1	0.03	—	—	—	—	255	2.06
May 22......	20	0.08	69	0.88	1	0.07	—	—	—	—	90	1.03
May 27......	15	0.06	92	1.23	5	0.12	—	—	—	—	112	1.41
June 3......	7	0.06	31	0.49	40	1.56	5	0.31	—	—	83	2.42
June 7......	2	0.08	36	0.48	59	2.73	12	0.90	—	—	109	4.19
June 11......	1	0.01	28	0.51	38	1.44	20	1.58	4	0.45	91	3.99
June 15......	4	0.03	35	0.40	42	1.46	14	0.98	8	0.86	103	3.73
June 19......	—	—	36	0.42	47	1.54	32	2.02	14	1.40	129	5.38
June 19......	—	—	28	0.22	34	1.09	26	1.75	15	1.45	103	4.51
June 25......	—	—	7	0.09	18	0.66	11	0.79	9	0.77	45	2.31
July 1......	—	—	3	0.05	14	0.52	6	0.48	10	1.30	33	2.35
July 5......	—	—	1	0.01	12	0.30	6	0.34	26	2.83	45	3.48
July 9......	—	—	3	0.07	10	0.39	15	0.98	49	4.80	77	6.24
July 16......	—	—	—	—	13	0.36	4	0.22	80	8.81	97	9.39
July 23......	—	—	—	—	6	0.15	5	0.15	64	6.24	75	6.54
July 30......	—	—	—	—	18	0.62	2	0.12	58	5.49	78	6.23
Aug. 12......	—	—	—	—	2	0.06	1	0.05	14.5	1.15	17.5	1.26
Mean Weight (mgm)....	3.84		11.91		36.39		67.11		101.14			

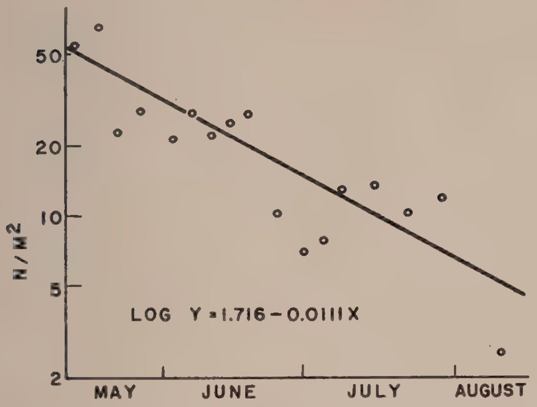

FIG. 1. A survivorship curve for *Orchelimum* fitted to population density at intervals during the summer of 1957.

the extent that adult female weights included eggs carried at the time of capture. Failure to consider egg production will result in an under-estimate of total production. To obtain total population production, the average weight of grasshoppers for each sampling period was calculated from the data of Table II, and multiplied by the mortality for that sampling period. The sum of the biomass lost by mortality was 1552 mg/m^2. At the end of the last sampling period, there were still 3.97 grasshoppers/m^2 remaining. Assuming that these grasshoppers became adults, they would have added another 402 mg for a total of 1954 mg. The caloric content of *Orchelimum* is shown in Table III; the mean figure of 5534 gcal/gm is used to convert production in biomass to 10.8 Kcal/m^2/yr. Different caloric values for different size groups of *Orchelimum* cannot be definitely established from the data in Table III, but there is at least a suggestion of increased caloric content with increasing age. Sexually mature *Daphnia pulex* are significantly higher in caloric content than young *Daphnia* (Richman 1958), and *Stenonema pulchellum* increases in caloric content with age (Trama 1958). Knowledge of the production for each sampling period would give an idea of trends in production rates throughout the season. Accordingly, the weight gain for the grasshoppers surviving each sampling period was calculated, using the mean weight of all the animals for the sample. The weight gain of the grasshoppers which died during each sample period, or one half of the weight gain of an average grasshopper during that period, multiplied by the number of grasshoppers dying, was added to the

TABLE III. Caloric content of *Orchelimum*, *Orchelimum* feces, and *Spartina*

	Number of samples	g cal/gm
Orchelimum: Adult	4	5590
Orchelimum: 15-20 mm	2	5798
Orchelimum: 10-15 mm	1	5302
Orchelimum: 5-10 mm	1	5033
Orchelimum: Feces	2	3522
Spartina: dead stems	2	3777
Spartina: entire plant	5	4028
Spartina: leaves	5	4113
Orchelimum (mean)		5536
Spartina (mean, living only)		4070

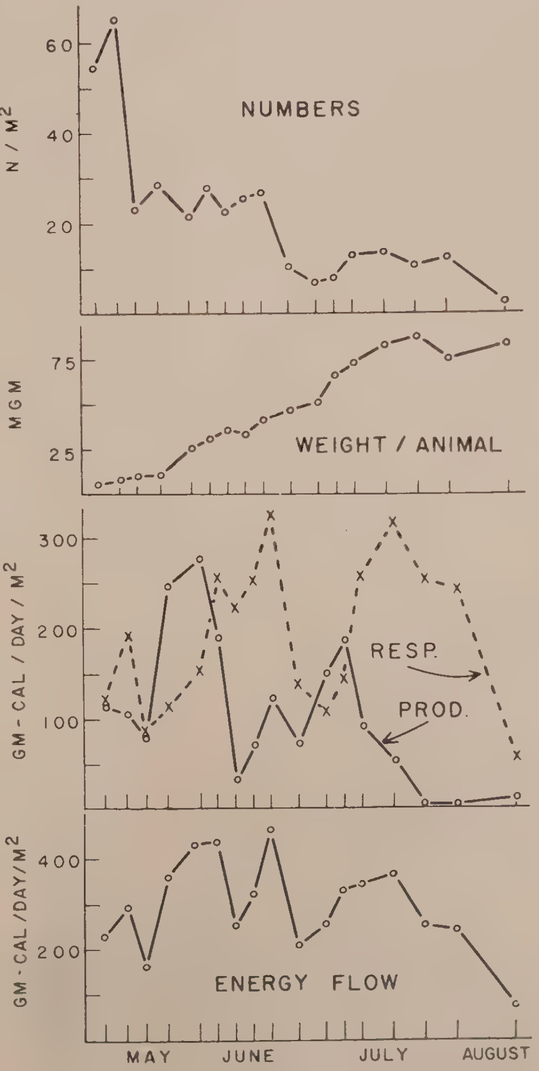

FIG. 2. Trends of numbers, biomass, respiratory and production rates, and energy flow of an *Orchelimum* population.

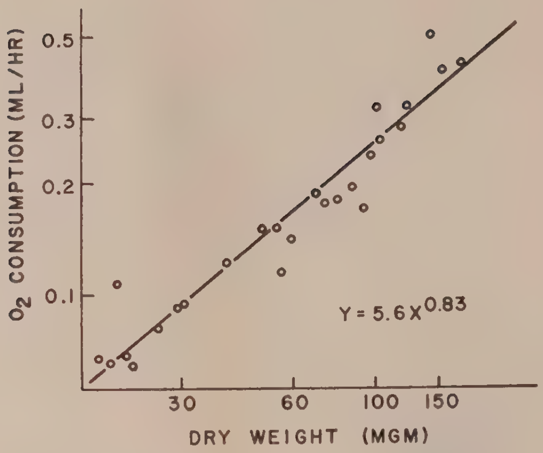

Fig. 3. Oxygen consumption of different sized *Orchelimum* at 30° C.

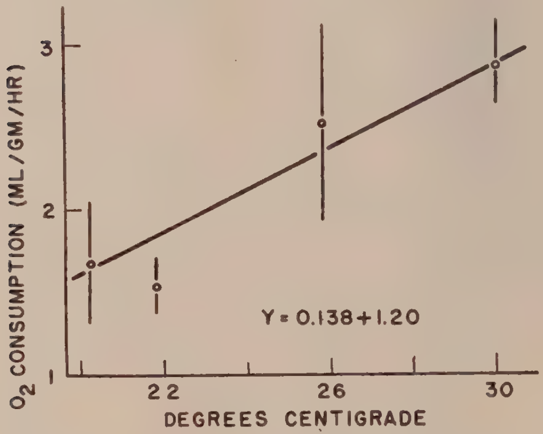

Fig. 4. Oxygen consumption of *Orchelimum* over the temperature range found in the marsh. Vertical lines are two standard errors on either side of the mean.

weight gain of the survivors. The resulting curve of production rate is shown in Fig. 2.

Fig. 3 shows the oxygen consumption rates of grasshoppers of different sizes, at 30°C. To estimate oxygen consumption of the population, the O_2 consumption rates of each size class of the population were determined by the regression of O_2 consumption on size (Fig. 3) and then applied to the census data, so that the O_2 consumption could be calculated for the grasshoppers in each sampling interval in ml $O_2/m^2/hr$. Figure 4 shows O_2 consumption rates of grasshoppers at temperatures from 20-30°C. Mean temperatures for the sampling periods were obtained from the weather station at the Marine Institute. The O_2 consumption rates at these temperatures, calculated from the curve in Fig. 4, were then expressed as a percentage of the rate at 30°C, and the population oxygen consumption rates for each sampling period were adjusted for the temperature prevailing at that time. The sum of the products of the temperature-corrected O_2 consumption and the hours in the sampling periods yields the total O_2 consumption for the population, which was 3.76 liters. The respiratory energy, after conversion by the coefficient 4.93 cal/ml O_2, was 18.6 kcal/m^2/yr. This will be an underestimate of the annual respiration, since some grasshopper activity was missed in early May and late August. The sum of production and respiration, or energy flow, for the grasshopper population over the annual cycle was 29.4 kcal/m^2.

The results of defecation experiments are shown in Table IV. Defecation plus assimilation equals ingestion, and by pooling the experiments, a ratio of assimilation/ingestion (E_a or assimilation efficiency) of 27.4% is found, with an experimental range of 20.8%-35.4%. When applied to the 1957 population, the result is an estimate of ingested *Spartina* of 107 kcal/m^2/yr.

Table IV. Ingestion rates of *Orchelimum*

Number of Animals		Assimilation cal/hr	Defecation cal/hr	Ingestion cal/hr	Assimilation Efficiency (%)
Adults	Nymphs				
2	—	2.95	7.04	9.99	29.5
10	—	20.00	65.16	85.16	23.5
11	—	22.59	36.98	59.57	37.9
10	—	18.82	71.50	90.32	20.8
13	—	26.78	68.68	95.46	28.0
11	—	22.54	55.30	77.84	29.0
—	14	15.54	46.14	61.68	25.2
—	18	23.38	71.14	94.52	24.7
—	11	14.60	30.29	44.89	32.5
—	8	10.38	18.95	29.33	35.4
Pooled values.........		177.58	471.18	648.76	27.4

Discussion and Conclusions

By converting production and respiration to a common unit of energy, it becomes possible directly to compare species populations at different trophic levels. The caloric content of *Spartina*, from 10 determinations kindly provided by Dr. C. E. Connell, is 4.07 kcal/gm. An estimate of 5200 kcal/m^2/yr has been made of the net production of *Spartina* in the type marsh where grasshoppers are most abundant (Smalley 1959).

The ratio of *Spartina* actually utilized by the grasshopper population (*i.e.*, energy flow) to that produced is thus about 0.57%. The *Spartina* ingested by the grasshoppers, which is assimilated with an efficiency of about 27% (Table III), amounts to about 2% of the net production of grass. The grass which is ingested and not assimilated does not enter into the energy balance of the population, but this process can be ecologically significant, since the grass is removed from the *Spartina* stems and deposited on the marsh or in the tidal waters in the form of feces, where it becomes available to a different group of organisms. Considering the whole marsh-estuarine system, the annual utilization efficiency of grasshoppers is low because *Spartina* grows throughout the year, at rates which vary with temperatures and marsh types in a complex pattern which has not yet been adequately described. Since the grasshoppers feed only on the leaf blade, and over a period of only 4 months, the utilization efficiency, on an annual basis, is reduced. In some degree, a low utilization efficiency reflects certain life history features of an organism—in the case of *Orchelimum fidicinium,* a short life span and the inability to utilize the culms and leaf sheaths of *Spartina.*

There are very few primary consumers which eat the living, growing grass. Besides *Orchelimum,* there are a few species of Fulgoridae which become quite abundant in the winter, and some flies whose larvae may eat *Spartina.* Most of the *Spartina* production is thus passed on to decomposers in the marsh and surrounding waters. Many of the most common marsh animals are detritus feeders, including the ubiquitous fiddler crabs (*Uca* spp.), the marsh mussel (*Modiolus demissus*) and the salt marsh periwinkle (*Littorina irrorata*). Teal (1959) found that considerable primary consumption of marsh grass may occur after growth and partial decomposition.

Some of the factors affecting energy flow in *Orchelimum* are shown in Fig. 2. Several processes are going on simultaneously; (1) the number of grasshoppers is decreasing, (2) the mean size and weight of individual grasshoppers is increasing, (3) respiratory rate per grasshopper is increasing, while at the same time decreasing per unit weight. Production is a direct consequence of (1) and (2), while the curve for respiration is compounded of the population density, size of individual animals and temperature. The population density, mean weight of the grasshoppers, and respiratory rate combine to determine the course of energy flow. The energy flow throughout the season, as a result of this complex of factors, shows less variation than the various population and physiological characteristics taken independently. For these reasons, the biology of the individual animals and the structure of the population will determine the nature of the seasonal course of energy flow.

ACKNOWLEDGMENTS

I am indebted to Dr. E. P. Odum for substantial assistance and advice. Mr. Smith Kimball helped in the field and laboratory during 1957, and Dr. C. E. Connell aided and advised with calorimetry. Dr. W. H. Cross identified *Orchelimum.*

SUMMARY

Population density, growth rates, respiratory rates, caloric content and rates of defecation were found for *Orchelimum fidicinium,* a grasshopper living in Georgia salt marshes. From these measurements, rates of ingestion, production, energy loss by respiration, and defecation were estimated for the population on an area basis.

Over an annual cycle of about 100 days, production was 10.8 kcal/m^2/yr, total energy flow was 29.4 kcal/m^2/yr and ingestion of *Spartina alterniflora,* the grasshoppers' sole source of food, was 107 kcal/m^2/yr.

Less than one % of the *Spartina* was eaten by *Orchelimum* in the area studied; there are few animals eating the growing *Spartina;* thus, most of the net primary production of the marsh is decomposed either in the marsh or in the surrounding waters.

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ECOLOGICAL STUDIES OF MARINE DERMATITIS-PRODUCING SCHISTOSOME LARVAE IN NORTHERN NEW ENGLAND[1]

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Schistosome dermatitis, recognized for over a quarter-century from fresh-water sources (Cort 1928, 1950), was first associated with the marine environment by Penner (1950), and was studied in New England by Stunkard and Hinchliffe (1952) and Sindermann and Gibbs (1953). Cercariae of the avian schistosome *Austrobilharzia variglandis* have been found to be responsible for human dermatitis along the coasts of Long Island, Rhode Island, Massachusetts, and Maine. The mud snail *Nassarius obsoletus* (*Nassa obsoleta*) serves as an intermediate host for the worm in this area, and several species of migratory birds have been implicated as definitive hosts, including the lesser scaup duck (Price 1929), red-breasted merganser (Penner 1953), black duck (Sindermann unpublished data), and probably others. Experimental infections have been obtained in canaries, pigeons, herring gulls, and domestic ducks (Stunkard and Hinchliffe 1952). Human dermatitis is acquired by contact with cercariae in inshore waters near mud snail aggregations, and is an occupational disease of clam diggers (Figure 1).

With the inclusion of the inshore marine environment as a potential cercarial contact area, the factors of salinity and intertidal habitat of the snail host have been added to ecological studies of dermatitis-producing schistosome larvae, and have been found to be important to the maintenance and limitation of the parasite (Sindermann 1956, Sindermann, Rosenfield and Strom 1957).

The present report is a continuation of an attempt to elucidate the relationship of the larval avian schistosome with its snail host in northern New England, and with changes in the physical environment. Particular attention has been directed toward two ecological aspects of public health significance:

(1) seasonal changes in larval schistosome incidence in mud snails, and

(2) the influence of environmental factors on emergence of schistosome cercariae.

Results reported here are based on both field studies and laboratory experiments, the latter conducted in the sea water tanks of the Fisheries Research Station and the Fisheries Biological Laboratory, Boothbay Harbor, Maine.

SEASONAL CHANGES IN INFECTION OF THE SNAIL HOST

This study is concerned with a parasite which alternates between two host populations—snail and bird—which participate in seasonal migrations. Thus it seemed quite probable that seasonal changes of incidence in the snail intermediate would occur, despite the fact that an earlier short-term investigation (Sindermann and Gibbs 1953) had failed to disclose supporting evidence. It is important to note in retrospect that the earlier survey involved snail samples taken from below the mean low tide line. Since later sampling indicated that incidences might vary depending on the location of the snails in relation to high and low tide zones, as well as with season, a 2-year study was made of the infection and the snail host on one tidal mud flat—Back Cove in Portland, Maine. This flat extends for over 1000 yards between mean high and low tide lines. Restriction to one area permitted monthly examination of samples from a series of inshore (high tide zone) and offshore (low tide zone) stations, as well as experimental studies. Examination was limited to snails with a shell length in excess of one centimeter. Whenever possible, a sample consisted of 300 snails, examined microscopically after crushing. Scarcity of snails and icing of flats prevented collection of high tide zone samples from November to April. To insure that the picture which emerged was typical and not peculiar to one mud flat, concurrent but less frequent observations were made on 2 other tidal flats—West Bath and Maquoit Bay. These flats were topographically different from the Portland Back Cove area studied.

Incidence in samples from high and low-tide zone stations on the Portland flat from January 1955 through December 1956 are presented in Figure 2.

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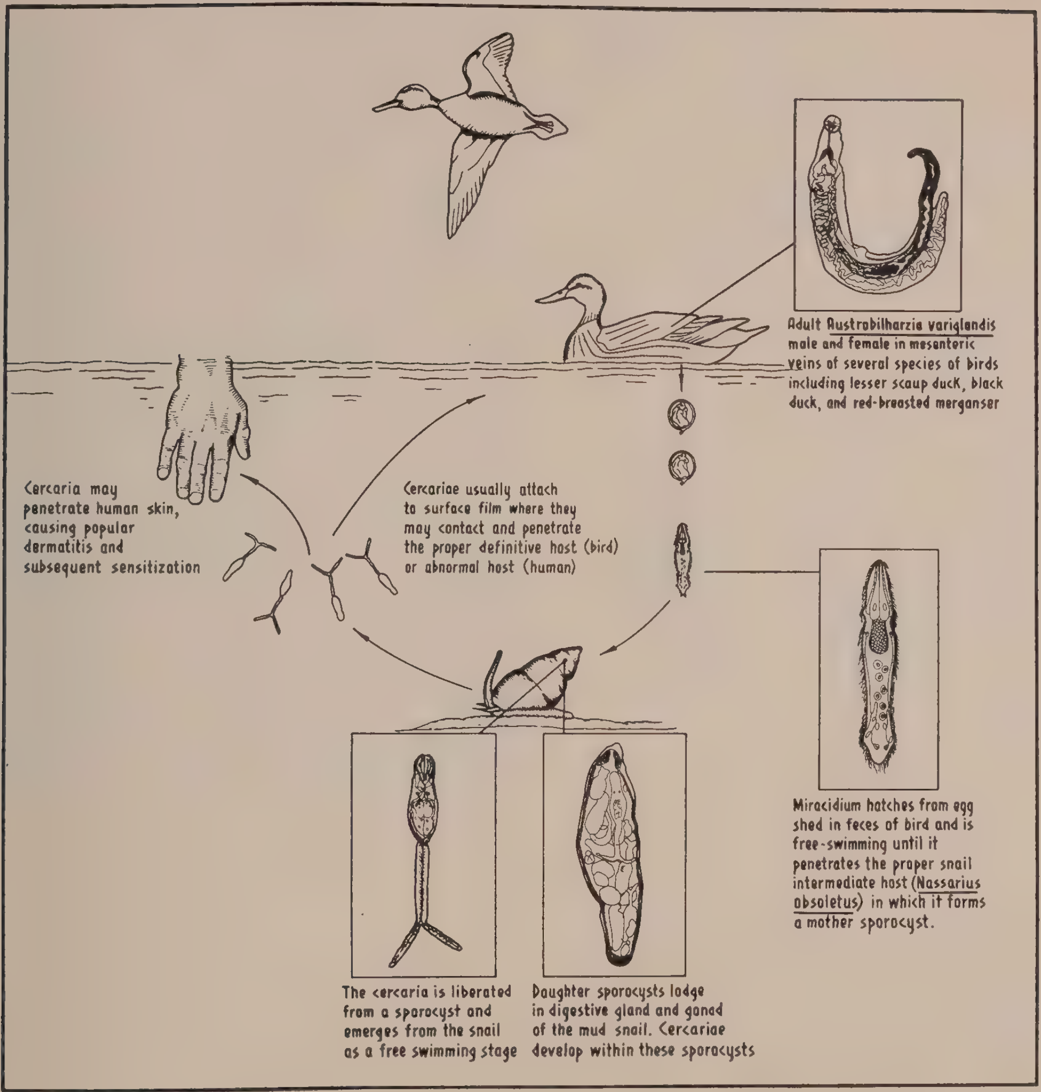
[1] The author wishes to express his thanks for the assistance of Alden Stickney, John Hurst, Aaron Rosenfield, Leroy Strom, Robert Sindermann, and others of the staffs of the Fisheries Research Station and the Fisheries Biological Laboratory, Boothbay Harbor, Me.

Research was supported in part by grant E-974 from the National Institutes of Health, United States Public Health Service.



Adult Austrobilharzia variglandis male and female in mesenteric veins of several species of birds including lesser scaup duck, black duck, and red-breasted merganser

Cercaria may penetrate human skin, causing popular dermatitis and subsequent sensitization

Cercariae usually attach to surface film where they may contact and penetrate the proper definitive host (bird) or abnormal host (human)

Miracidium hatches from egg shed in feces of bird and is free-swimming until it penetrates the proper snail intermediate host (Nassarius obsoletus) in which it forms a mother sporocyst.

The cercaria is liberated from a sporocyst and emerges from the snail as a free swimming stage

Daughter sporocysts lodge in digestive gland and gonad of the mud snail. Cercariae develop within these sporocysts

FIG. 1. The life cycle of *Austrobilharzia variglandis* in northern New England. Details of this life cycle were worked out by Stunkard and Hinchliffe (1952) and figures of adult, sporocyst, and cercaria have been redrawn from their paper. The figure of the miracidium has been redrawn from Chu and Cutress (1954).

Examination of these data has indicated that:

(1) larval schistosome infections were significantly more abundant in snails sampled at inshore (high tide zone) stations than at offshore (low tide zone) stations;

(2) incidence in inshore samples increased through the summer and reached a peak in autumn; and

(3) infections at low tide zone stations were consistently low, with only slight increases in April and October.

Investigation of the seasonal migrations of the snail population has also contributed to an understanding of changes in incidence. Seasonal movements of this mollusc in northern New England have not been well-documented, although they have been noted for other areas by Batchelder (1915) and Jenner (1956, 1957). Observations, aided by marking experiments, during the present study indicated that many snails overwintered in dense, quiescent, subsurface aggregates of hundreds to thousands, usually near or below mean low tide line (Figure 3). In April and May these

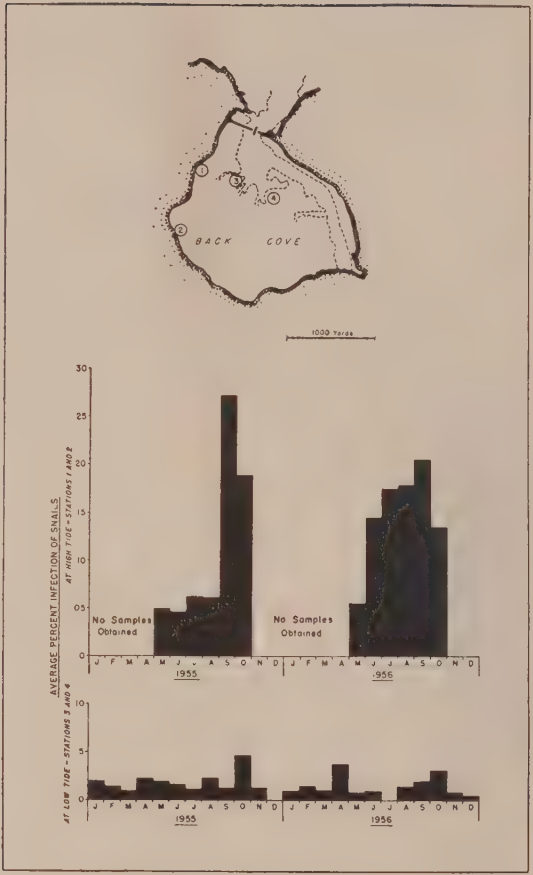


FIG. 2. Back Cove, Portland, Maine, with average monthly incidence of *Austrobilharzia* at high and low tide zone stations.

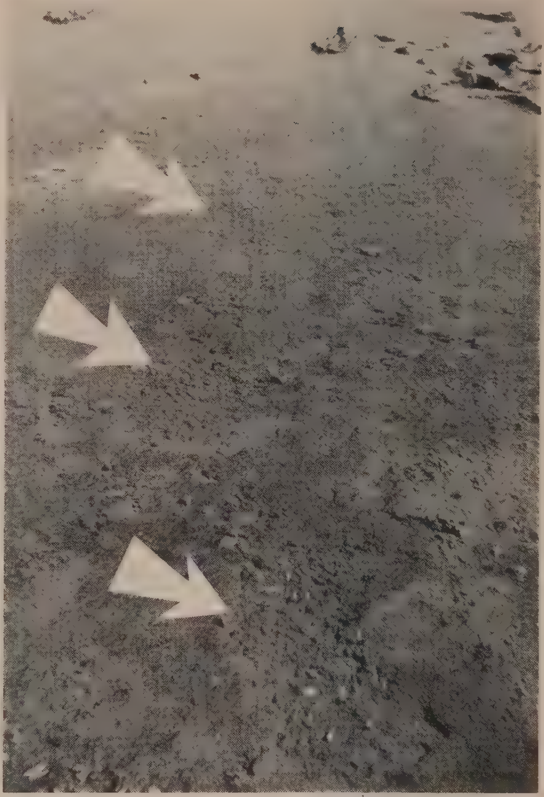


FIG. 3. Three winters subsurface aggregates of *Nassarius obsoletus*. Each is approximately 20 inches in diameter and contains several hundred snails, although larger and smaller aggregates occur.

aggregates began to disperse and many member snails moved over the surface of the flat and up intertidal runoff streams toward the high tide zone, arriving there during late May and remaining throughout the summer. Individuals could be found on the open flat or concentrated about tidal runoff streams in the high tide zone. Egg capsules were produced from June to August. Retreat to the low tide zone begin in September, and by November most snails had again become part of dense quiescent offshore aggregates.

Examination of monthly changes in worm incidence, together with observations of differentially marked infected and unifected snails, indicated that parasitization by *Austrobilharzia variglandis* and certain other larval trematodes (*Zoogonus rubellus* and *Himasthla quissetensis* especially) retarded or inhibited normal offshore movement of the host in autumn—contributing to relatively heavy inshore incidence at this time of year, and leaving the infected snails in the progressively unfavorable environment of the high tide zone in winter. Schistosome infections acquired in autumn began to mature in March, while those acquired in spring began to mature in July. Thus, in late summer and early autumn, snails infected in spring of the current year and in autumn of the previous year contributed to the parasitized segment of the population. This, combined with differential movement of infected and uninfected snails, seemed to provide a basis for a peak of infection in autumn. Pre-existing larval schistosome infections tended to be reduced in winter, in numbers seemingly dependent on the severity of the winter. Mature infections that persisted through the cold months were observed to decrease in vigor by the following July, being characterized by flaccid sporocysts and few cercariae.

Figure 4 summarizes the seasonal sequence of events pertaining to schistosome infections and movements of snails on the study flat.

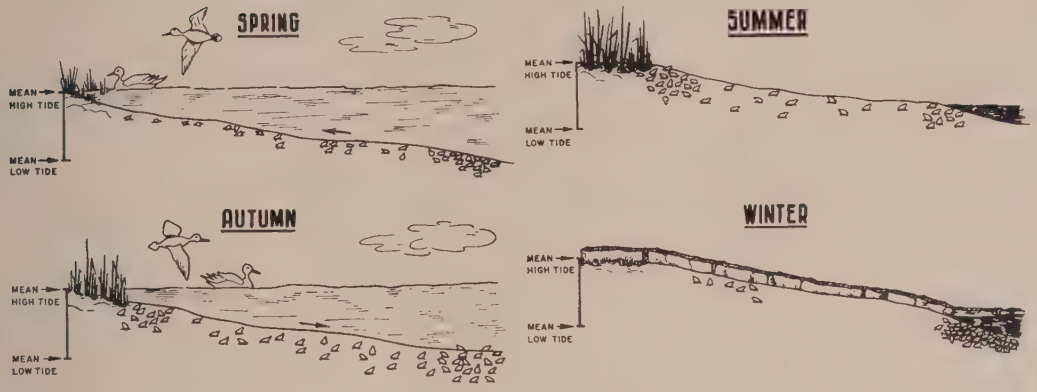


FIG. 4. a. The mud flat in spring. Many *Nassarius* move from low tide zone aggregates toward the high tide zone, while migratory birds congregate in inshore areas, providing a source of infection for snails. Infections which survived from the previous summer begin emitting cercariae when water temperature exceeds 10°C, and infections acquired during the previous autumn mature.

FIG. 4. b. The mud flat in summer. *Nassarius* aggregate in the high tide zone, particularly near intertidal runoff streams, although some snails may be found on the surface of the flat and in the low tide zone. Incidence of larval schistosomes in high tide zone snails rises throughout the summer. Infections acquired in spring mature by midsummer, while infections which survived from the previous summer decline in activity.

FIG. 4. c. The mud flat in autumn. Uninfected *Nassarius* move from the high tide zone over the flat or down intertidal runoff streams toward winter aggregation sites in the low tide zone, but snails with schistosome and other trematode infections tend to remain in the high tide zone. Incidence of larval schistosome infections in inshore areas is highest of the year.

FIG. 4. d. The mud flat in winter. The flat is ice covered intermittently or constantly from December to March, and is scoured during late winter thaws. *Nassarius* are quiescent in dense aggregates of hundreds to thousands below the surface of the mud in the low tide zone, although occasional small clusters of infected snails may be found in mid or high tide zones. Schistosome infections acquired in autumn develop slowly and begin to mature by March.

EXPERIMENTAL STUDIES OF FACTORS INFLUENCING CERCARIAL EMERGENCE

With some knowledge of the seasonal nature and extent of parasitization, it was felt that if the factors controlling release of dermatitis-producing cercariae from infected snails could be determined, it would be possible to assess the potential human danger wherever *Nassarius* were abundant. Considering the intertidal mud-flat habitat of the snail host, certain ecological conditions might limit or enhance cercarial emergence:

(1) salinity—varying with stage of tide, daily, or seasonally;

(2) temperature—varying daily and seasonally;

(3) oxygen tension—varying with stage of tide;

(4) nutrition of the host snail—varying daily or seasonally.

These have been examined experimentally, recognizing that other factors may also prove to be important. Whether changes in the environment of the snail influence cercarial release by acting directly on emerging cercariae or indirectly through the metabolism of the host has not been explored fully, although some indications have been found that changes in host metabolism may influence the rate of cercarial release.

Effect of changes in salinity

Salinity effects on the rate of cercarial emergence were pronounced. Parasitized snails in groups of 25 were kept at 20°C in graded salinities from 5 to 30 $^{0}/oo$, and emergence from each snail recorded daily for 2 months. It was found that greater percentages of parasitized snails emitted cercariae and that the average rate of cercarial emergence was greatest at salinities between 15 and 25 $^{0}/oo$, with reductions above and below these concentrations (Table I).

TABLE I. Emergence of Cercariae of *Austrobilharzia variglandis* at Various Salinities

Salinity in Parts per Thousand	Percent of Infected Snails Emitting Cercariae	Average Daily Rate of Cercarial Emergence per Snail
5	22	12
10	77	61
15	84	136
20	87	155
25	88	159
30	74	70

It is interesting and perhaps pertinent that, in a later study, curves drawn for oxygen consumption of parasitized *Nassarius* in the same graded salinities essentially paralleled the curves for emergence, with greatest oxygen consumption in the middle salinities and reduction at either end of the salinity gradient (Sindermann and Rosenfield 1957).

Effect of temperature

Low temperatures reduced or inhibited cercarial emergence. Parasitized snails were maintained in the laboratory in running sea water with seasonal light and temperature, and cercarial emergence was checked weekly throughout autumn, winter and spring. Emergence declined in autumn when the water temperature fell below 12°C, and ceased altogether between 6 and 8°, to resume again the following spring when these temperatures were exceeded. Cercarial emergence from snails could be stimulated at any time throughout the winter by placing them in sea water above 10°C.

Effect of environmental oxygen tension

It was observed early in the investigation that when parasitized snails were crowded, or held in specimen jars without frequent changes of sea water, cercarial emergence declined drastically—suggesting that availability of oxygen in the host environment might influence the rate of cercarial emergence. Although measurements of oxygen consumption of parasitized *Nassarius* in decreasing environmental oxygen tensions were not made, artificially increased oxygen tension in water in which infected snails had been crowded resulted in much higher emergence than from control groups without added oxygen.

Effect of host starvation

Parasitized snails were maintained without food in filtered sea water (changed daily) at a constant temperature of 20°C and the emergence from each snail counted daily for 45 days. Within a week from the start of the experiment cercarial emergence assumed a definite periodicity, with peaks every 3 to 4 days, and with little emergence during the intervening time. With few exceptions, the "bursts" of emergence occurred simultaneously in most snails under observation. This experiment was first carried out in the autumn of 1955 and repeated in the summer of 1956, with comparable results. In separate experiments, feeding starved snails after 15 or 30 days resulted in massive cercarial emergence within 48 hours.

Discussion

The avian schistosome *Austrobilharzia variglandis* completes its life cycle in northern New England in a highly mobile situation, involving migratory intermediate and definitive hosts. Parasitization of the snail intermediate has the effect of immobilizing it, at least temporarily, in inshore areas. This increases the opportunity for infection of the definitive host during its autumn migration, but also limits the parasite through death of some of the infected snails thus immobilized in the progressively unfavorable high tide zone.

The seasonal changes in abundance of *Austrobilharzia,* as observed for 2 years, can thus be related to migrations of hosts, extent of infection of hosts, and survival or death of parasitized snails. Higher inshore incidence may be explained by closer proximity of intermediate and definitive hosts. High autumn inshore incidence can result from the simultaneous presence of infections from the previous autumn and the current spring, and from differential movements of normal and parasitized snails. Yearly variations in infection of *Nassarius* have been noted also, but have not been studied in detail. These are probably related to differential survival of parasitized snails through mild or severe winters, and to yearly variations in infection and movements of migrant definitive hosts.

Mere assessment of larval schistosome incidence in snails from any locality does not provide adequate information about the risk of dermatitis unless numbers of emerging cercariae can also be estimated. Environmental variables are known to affect release of trematode cercariae. Cort (1950), in reviewing the status of knowledge of fresh-water schistosome dermatitis, noted that seasons and such physical features of the environment as light and temperature were important in determining risk of dermatitis. Brackett (1940) studied factors influencing emergence of fresh-water schistosome cercariae and found that a rapid increase in temperature increased the rate of emergence. Olivier *et al.* (1953) found that emergence of *Schistosoma mansoni* cercariae from *Australorbis glabratus* was greatly reduced under conditions of anaerobiasis or low environmental oxygen. Kuntz (1947), also working with *S. mansoni,* concluded that temperature was an important factor in cercarial emergence. Rees (1948) studied the effects of light, temperature, and salinity on emergence of the marine larval trematode *Cercaria purpurae* and found that light enhanced emergence, while any changes from normal salinity were inhibitory.

The investigation reported in this paper has suggested that both salinity and temperature influence emergence of *Austrobilharzia variglandis* cercariae, and that other factors, such as host nutrition and environmental oxygen tension, may also be important. With knowledge of seasonal changes in abundance of infections, and with some understanding of the causes of increased or decreased cercarial emergence under experimental conditions, prediction of risk of marine schistosome dermatitis seems possible.

SUMMARY

Two aspects of the ecology of *Austrobilharzia variglandis,* a marine dermatitis-producing avian schistosome, have been investigated: (1) seasonal changes in infection of the snail intermediate host (*Nassarius obsoletus*) at different levels of an intertidal mud flat, and (2) the influence of environmental factors on rate of cercarial emergence.

Parasite incidence exhibited definite seasonal changes in inshore (high tide zone) snail samples, increasing in summer and reaching a maximum in early autumn. Incidence in samples from the low tide zone remained low (less than 5%) throughout the year, with only slight increases in April and October, and was always lower than in samples from the high tide zone.

Uninfected *Nassarius* migrated between the high and low tide zones, moving inshore in spring and retreating in autumn. Larval schistosome infection retarded or inhibited the autumn offshore migration of the snail host, causing high inshore incidence when migratory birds were most abundant in the area, but also providing a possible mechanism for limiting the infection in the snail population by immobilizing parasitized snails in the unfavorable high tide zone during the winter.

Experimental studies of cercarial emergence demonstrated that maximum emergence occurred in salinities of from 15 to 25 $^{0}/oo$. Temperatures below 12°C reduced cercarial emergence, while those below 6° inhibited emergence completely. Starvation of the host snail resulted in decline in cercarial emergence and the appearance of a 3-4 day period between "bursts" of cercariae, while feeding of starved snails was followed by massive emergence within 48 hours.

When observations on season and location of highest and lowest larval schistosome incidence in mud snails are combined with results of experimental studies of environmental influences on cercarial emergence, it should be possible to determine the risk of human infection wherever *Nassarius* are abundant.

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THE ECOLOGICAL SIGNIFICANCE OF CLADOCERAN REMAINS IN LAKE SEDIMENTS[1]

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Exoskeletal remains of Cladocera occur abundantly in lake sediments from at least late-glacial time to the present. Relatively few major studies of these remains have been published (reviewed by Frey 1958), and appreciation of their abundance and potential significance is not yet widespread among limnologists or ecologists. In part this has resulted from the difficulty of identification. Only rarely is a complete animal preserved. Usually the various components of the exoskeleton (head shields, shells, postabdomens, claws, antennules, antennal segments, and ephippia) are separated from one another. However, among the family Chydoridae in particular the species are sufficiently differentiated morphologically to enable positive identification from the fragments of the exoskeleton when reference material is available for comparison.

In previous studies (Frey 1958, 1960a) I have obtained the distinct impression that probably all species of chydorids, and to a lesser extent the other Cladocera as well, occurring in a body of water become represented by morphological remains in the sediments. To test this hypothesis the lakes at Madison, Wisconsin, were selected as the best or among the best known lakes of the world with respect to their Cladocera. E. A. Birge studied the Cladocera and plankton of the Madison lakes for more than 30 years before shifting his major attention to other aspects of limnology. His list of Cladocera occurring in these lakes (Birge 1892) is the basis of comparison for the present report. No additions to this list occur in his later papers (Birge 1893, 1910, 1918), nor could any unpublished records be found in the Birge archives at Madison.

The quantitative aspects of the present study were of secondary importance initially, because only one sample of sediment was available from each lake. However, the results obtained from even these limited samples seem so closely related to the known limnology of the lakes and the morphometry of the basins that they suggest a number of interesting ecological relationships.

Methods

On November 17 and 22, 1958, surface samples of offshore sediments were collected with a 6 x 6-inch Ekman dredge from the 5 lakes at the following approximate water depths: Mendota, 30 ft; Monona, 40 ft; Waubesa, 25 ft; Kegonsa, 25 ft; Wingra, 15 ft. In each instance 2 Ekman samples were emptied into a bucket, allowed to settle for 5-10 minutes, and, after the excess water had been decanted, a two-quart jar was filled with the material. Assuming a sedimentation rate of about 2-3 mm a year, the 6 inches of surface sediments sampled would represent the accumulation of the past 50-70 years.

In the laboratory each sample was thoroughly mixed, after which 1-cc aliquots were removed. One such aliquot was used for obtaining wet weight, dry weight, ash weight at 550°C (in a muffle furnace), and ash weight at approximately 1000-1200°C (over a Meeker burner).

Another aliquot was allowed to react with hot 10% HCl on a magnetic stirrer hot plate until all ebullition of CO_2 had ceased. After being centrifuged and washed with distilled water, the sample was treated with hot 10% KOH on a magnetic stirrer hot plate for approximately 30 minutes. The material was washed again, and diluted to a volume of 15 ml, from which 0.05 ml subsamples were withdrawn with a bulb delivery pipette calibrated in 0.01 ml. Each subsample representing 1/300 of the original aliquot was mounted in glycerine jelly under a 22-mm coverslip. These are the quantitative preparations which enable the abundance of microfossils to be related to various sediment parameters.

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[1] Contribution No. 697 from the Department of Zoology, Indiana University. The author is indebted to Dr. A. D. Hasler for arranging for one of his students, Daniel J. Faber, to collect the desired sediment samples. Analysis of the material was accomplished in part through funds provided by NSF Grant G-6157, with Wayne P. Mueller helping greatly in preparation of the material. A condensed version of this paper was presented before the National Academy of Sciences in November, 1959 (Frey 1960b).

The material remaining after preparation of the quantitative samples was washed through a metal screen with mesh openings of approximately 80 µ. From small portions of the suspended residue examined at a stereoscopic magnification of 45 diameters, individual skeletal fragments were picked out with a needle and mounted in polyvinyl lactophenol stained with lignin pink. These preparations are for qualitative purposes only, although it will be apparent from consideration of the results that they also give a rough idea of the relative abundance of the various species.

The remains were identified by comparison with intact specimens of the various Cladocera and also by comparison with identified remains and complete exuviae accumulated from previous studies (Frey 1958, 1959, 1960a).

QUALITATIVE RESULTS

Birge (1892) listed 65 species and subspecies of Cladocera from the Madison lakes, distributed among 8 families. Identification of the remains of these species in the sediments is complicated by the fact that not all Cladocera are preserved equally well in sediments. Among the Daphnidae only postabdominal claws, sometimes with the postabdominal teeth still attached, mandibles, and ephippia occur. Among the Sididae, *Sida crystallina* has been positively identified from a postabdominal claws, postabdomens, mandibles and antennal segments, and *Latona setifera* from the basal exopod segment of the antennae. There is a possibility that other genera such as *Diaphanosoma* may also be represented by mandibles and antennal segments, but positive identifications have not yet been accomplished. The Macrothricidae almost never are found. Identification of species of these families from skeletal fragments is very difficult at the present stage of our knowledge.

Three families are represented by only one species each in the Madison lakes. Although *Holopedium gibberum* was not found in the present study, it might be expected to occur because postabdomens and claws of the related *Holopedium amazonicum* have been found in Pages Lake, North Carolina (Frey unpublished). Birge collected *Holopedium* only once at Madison. Remains of *Polyphemus* have never been reported

TABLE I. Chydorids known to occur in the Madison Lakes. Those designated by an asterisk were not reported by Birge (1892)

Species now known to occur	Name used by Birge, if different	Authority for change
1. *Eurycercus lamellatus* (O. F. Müller) 1785		
2. *Camptocercus rectirostris* Schödler 1862	*Camptocercus biserratus* Schödler 1862	Lilljeborg (1900)
3. *Camptocercus lilljeborgi* Schödler 1862	*Camptocercus macrurus* (O. F. Müller) 1785	Wagler (1937)
4. *Acroperus harpae* (Baird) 1835	*Acroperus leucocephalus* (Koch) 1841	Baird (1850)
5. *Kurzia latissima* (Kurz) 1874	*Alonopsis latissima* Kurz 1874 *Alonopsis media* Birge 1879	Dybowski & Grochowski (1894) Herrick & Turner (1895)
6. *Oxyurella tenuicaudis* (Sars) 1862	*Alona tenuicaudis* Sars 1862	Dybowski & Grochowski (1894)
7. *Graptoleberis testudinaria* (Fischer) 1848		
8. *Leydigia leydigi* (Schödler) 1863	*Leydigia quadrangularis* (Leydig) 1860	Schödler (1863)
* 9. *Leydigia acanthocercoides* (Fischer) 1854		
10. *Alona affinis* (Leydig) 1860		
11. *Alona quadrangularis* (O. F. Müller) 1785	*Alona lepida* Birge 1892	Birge (1918)
12. *Alona rectangula* Sars 1861	*Alona lineata* (Fischer) 1854 = *A. pulchra* Hellich, according to Matile	Birge (1892) & Lilljeborg (1900)
13. *Alona guttata* Sars 1862		
14. *Alona costata* Sars 1862		
*15. *Monospilus dispar* Sars 1861		
16. *Alonella exigua* (Lilljeborg) 1853	*Pleuroxus exiguus* (Lilljeborg) 1853	Kurz (1874)
17. *Alonella excisa* (Fischer) 1854	*Pleuroxus excisus* (Fischer) 1854	Kurz (1874)
*18. *Alonella nana* (Baird) 1850		
*19. *Alonella rostrata* (Koch) 1841	Not *Alonella rostrata* of Birge (1918)	(see Frey 1959)
20. *Dunhevedia crassa* King 1853	*Dunhevedia setigera* Birge 1879	Keilhack (1909)
21. *Pleuroxus denticulatus* Birge 1879		
22. *Pleuroxus procurvus* Birge 1879	*Pleuroxus procurvatus* Birge 1879	Birge (1879)
23. *Pleuroxus striatus* Schödler 1863	*Pleuroxus gracilis* Hudendorff 1876, var. *unidens* Birge 1879	Birge (1918)
24. *Pleuroxus trigonellus* (O. F. Müller) 1785		
*25. *Pleuroxus aduncus* (Jurine) 1820		
26. *Chydorus globosus* Baird 1850		
27. *Chydorus sphaericus* (O. F. Müller) 1785		
*28. *Chydorus faviformis* Birge 1893		
29. *Anchistropus minor* Birge 1893	*Anchistropus* sp.	

from sediments. Caudal furcae and mandibles of *Leptodora kindti* occur quite commonly in lake sediments, and were found in this study.

Only the Bosminidae and Chydoridae are represented by head shields and shells in addition to other types of remains; hence these families are best suited for identification of species. The genus *Bosmina* is difficult to work with, even with intact specimens, because of the present confusion in its taxonomy, the relatively obscure characters used to separate species, and the great seasonal morphological variation (cyclomorphosis). The Chydoridae, on the other hand, have a large number of species well differentiated morphologically, so that identification can be readily accomplished from skeletal fragments. The major emphasis in the qualitative portion of this paper is on the chydorids.

Table I presents the names of the chydorids currently known to occur in the Madison lakes with authority for any changes in the names as used by Birge (1892), and Table II presents the results of the qualitative examination of the sediments.

The most significant part of the qualitative study is that all the chydorids listed by Birge were recovered from the sediments except *Dunhevedia crassa* (which he collected only in Lake Wingra) and probably *Oxyurella tenuicaudis,* and that 6 additional species not listed by Birge were found.

There is the possibility, of course, that some of these species may have become established in the lakes between Birge's time and the present, although this does not seem too likely. Where extensive climatic changes have occurred with a great influence on the trophic level of a lake, marked changes in the species composition of the chydorid population have been demonstrated (Frey 1958). However, during the past century climatic changes although progressive have been relatively slight, and under such conditions the composition of the chydorid population of a lake is quite stable (Frey 1960a). Possibly the increasing trophic levels of the Madison lakes have enabled additional chydorids to become established, although this, too, should be discounted until definitely established by stratigraphic analysis of the sediments.

Where *Leydigia leydigi* is so abundant, the small representation of the closely related *L. acanthocercoides* could certainly be overlooked. *Monospilus dispar, Alonella nana,* and *A. rostrata* obviously occur in very small populations, so that finding them in collections of living animals would be largely a matter of persistence and luck. *Pleuroxus aduncus* is abundant in Waubesa and Kegonsa, but these are the lakes Birge studied least intensively. *Chydorus faviformis* was not described until a later paper (Birge 1893).

TABLE II. Occurrence of Cladocera in the qualitative preparations from the Madison lakes. The figures are not strictly representative of the populations since special effort was made to recover the less common species. Of the chydorids listed by Birge (1892), only *Dunhevedia* was not recovered in the present study. Species designated by an asterisk were not reported by Birge

	Mendota	Monona	Waubesa	Kegonsa	Wingra	Totals
Sida crystallina	4	1	5	1	16	27
Latona setifera	—	—	1	—	1	2
Daphnia sp.	17	29	18	12	10	86
Ceriodaphnia sp.	8	2	5	1	10	26
Bosmina sp.	19	43	30	56	78	226
Leptodora kindti	2	29	9	14	4	58
Eurycercus lamellatus	10	24	30	15	43	122
Camptocercus rectirostris	21	43	58	28	40	190
Camptocercus lilljeborgi	—	—	1	—	—	1
Acroperus harpae	20	65	63	41	24	213
Kurzia latissima	—	2	3	—	3	8
Oxyurella tenuicaudis	1	4	2	5	1	13
Graptoleberis testudinaria	2	10	20	14	17	63
Leydigia leydigi	97	83	171	151	153	655
**Leydigia acanthocercoides*	2	—	4	1	4	11
Alona affinis	58	33	45	44	36	216
Alona quadrangularis	227	97	159	102	209	794
Alona rectangula	7	35	100	46	54	242
Alona guttata	—	—	—	—	1	1
Alona costata	—	—	—	—	1	1
**Monospilus dispar*	4	—	—	—	—	4
Alonella exigua	2	—	9	1	—	12
Alonella excisa	7	7	14	10	70	108
**Alonella nana*	—	—	—	—	1	1
**Alonella rostrata*	—	—	1	—	6	7
Dunhevedia crassa	—	—	—	—	—	0
Pleuroxus denticulatus	4	28	24	17	22	95
Pleuroxus procurvus	4	20	5	8	13	50
Pleuroxus striatus	1	—	—	—	—	1
Pleuroxus trigonellus	4	1	2	—	1	8
**Pleuroxus aduncus*	—	1	81	28	1	111
Chydorus globosus	4	—	6	2	6	18
Chydorus sphaericus	367	129	78	181	270	1025
**Chydorus faviformis*	—	—	—	—	4	4
Anchistropus minor	—	—	1	—	—	1
Unrecognizable chydorids	14	41	41	17	24	137
Total remains examined	906	727	986	795	1123	4537
Species of chydorids	19	16	22	17	23	29

At the time of his paper (1892) Birge stated:

> "The subjoined list also shows the value of long and careful collecting in one locality, and the impossibility of justly estimating the Cladocera of a lake from a single visit. The different forms behave much like the plants of a locality. Some species are present throughout the season. Some can be found only for a few days. Some come in the spring and disappear early, while others belong to the latter part of the open season. Of the nearly sixty species found in Lake Wingra I have never found more than thirty as a result of a single day's work. It is clear that a list of Cladocera compiled from a flying visit to a locality and containing from six to twenty species has no claim to represent the fauna of the locality. Only careful collecting at intervals throughout an entire

season can give even an approximate idea of the number of species present."

To this statement should be added that even careful and intensive collecting in restricted localities over a number of years does not necessarily provide a complete knowledge of the species present. A list of species, at least of chydorids, occurring in a given body of water can be obtained with least expenditure of time and greatest assurance of completeness from an examination of the sediments. Such a list can then serve as a guide in searching for and collecting the living animals.

In spite of the fact that *Dunhevedia crassa* was not recovered from Lake Wingra, there is no evievidence of any differential destruction of the various species of chydorids in sediments. Shells and heads of this species have been identified in our laboratory from the sediments of Winona Lake, Indiana, and of the Chuska Mountain lakes in Arizona-New Mexico.

In Table II it is obvious which species are abundant and generally distributed, and which species appear to be limited in distribution or abundance. Birge (1892) collected 60 of the 65 species and varieties from Wingra, but only 38 from Mendota. No figures are given for the other 3 lakes, and there is no indication as to which particular species occurred in Mendota. Hence, one cannot determine from Birge's paper if there is a progressive increase in number of species from the largest and deepest lake (Mendota) to the smallest and shallowest (Wingra). The number of species of chydorids recovered in the present study does not show such a progression, although Wingra does have the greatest number. Based on Birge's list and the present study, all 29 species of chydorids listed in Table II have been collected in Wingra.

The chydorids listed as unrecognizable contain those that were mounted in such a way the specific characters could not be recognized, and those that could be identified only to genus. It is not believed that any additional species occur in the population examined.

One of the interesting and significant aspects of these results is that although the chydorids are primarily substrate organisms associated with aquatic vegetation, macroscopic debris, and surface sediments in the littoral zone (Weigold 1910), their exoskeletal fragments occur abundantly in the offshore deep-water sediments of lakes. This relationship has been observed not only for small lakes, such as Linsley Pond (Deevey 1942), Schwarzsee (Brehm *et al.* 1948), Wallensen (Frey 1958), and Schleinsee (Frey 1960a) but also for lakes as large as Windermere (Scourfield 1943). Quite clearly the small buoyant fragments of these organisms are readily transported throughout the lake during periods of major circulation. Recent studies by Tutin (1955) and Gorham (1958) indicate that suspension of flocculant surface sediments during storms and overturn can be of considerable magnitude and significance. Hanson (1952) determined that the mean settling rate of flocs in the Mendota sediments is about 4 mm per second, which is considerably less than the magnitude of currents often observed in deep water (based on unpublished data of Bryson and Suomi). The extent to which offshore sediments faithfully reflect the populations of littoral Cladocera is currently being investigated in our laboratory.

PROXIMATE CHEMICAL ANALYSIS OF THE SEDIMENTS

In the quantitative study, sediment parameters were determined simply from the dry weight, the loss on ignition at 550°C in a muffle furnace, and the additional loss on ignition at Meeker burner temperature (*ca.* 1000-1200°C). The loss on ignition at 550° is interpreted as the organic content, and the additional loss on ignition at the higher temperature as chiefly the CO_2 from $CaCO_3$ and $MgCO_3$. $CaCO_3$ does not begin to give up its CO_2 until a temperature of about 825°C. $MgCO_3$ does so at lower temperatures, but since the Mg content of the sediments is low (Birge and Juday 1911, Black 1929, Twenhofel 1933, 1937), there is little error involved. The calculated $CaCO_3$ content subtracted from the ash weight at 550° leaves a residue consisting mainly of SiO_2, but also including Al_2O_3 and Fe_2O_3. According to more exact chemical analyses already published (Birge and Juday 1911, Twenhofel 1933, 1937), there is only a small clay content in the surface sediments, and hence little error is involved from loss of water from clay minerals. Hansen (1959) reviewed the various methods of determining the organic content of sediments and concluded that, especially when the clay content is low, loss on ignition gives the most reliable estimate.

The percentage compositions of the 5 sediment samples according to these parameters are given in Table III. That these figures are approximately correct and at least sufficiently accurate for the present purpose is demonstrated by comparison with the few previously published analyses. Birge and Juday (1911) present a single analysis for Lake Mendota sediments, in which loss on ignition (= organic matter and CO_2) is 41.99%, CaO 33.21%, and MgO 2.16% of the dry weight. Conversion of these figures yields 63.8% $CaCO_3 + MgCO_3$, and 13.6% organic matter, leaving a "residue" of 22.6%. The organic content agrees closely with the value of the present study, but the carbonate content is considerably higher. However, Twenhofel (1933) pointed out that the Ca content of the deeper consolidated sediments (such as the sample of Birge and Juday) is greater than in the softer surface ooze. He found that the carbonate content of offshore surface ooze in 42 to 68 feet of water varied from 29 to 45%. In Twenhofel's transect 2 the ooze layer was not analyzed, but the top of the underlying consolidated layer yielded a carbonate content of 55.6% and an organic content of 14.9% by the definitions used here. More recently Murray (1956) found that the average carbonate content of the surface sludge (= unconsolidated dark surface sediment) where it rests on the underlying marl is 32.2%, and the average organic content (determined by chromic acid digestion and back titration with ferrous ammonium sulphate) is 13.2%.

TABLE III. Approximate composition of the surficial deep-water sediments of the Madison lakes, based on 1 cc of fresh sediments. Organic content represents loss on ignition at 550°C. $CaCO_3$ is the additional loss resulting from Meeker burner incineration (ca. 1000-1200° C) multiplied by 2.2742. Residue represents the dry weight minus organic content and $CaCO_3$

Lake	WEIGHT (g) OF 1cc SEDIMENTS		% water	% COMPOSITION DRY SEDIMENT		
	Wet	Dry (95° C)		Organic	$CaCO_3$	Residue
Mendota	1.1122	0.2168	80.5	15.0	42.4	42.6
Monona	1.0964	0.1884	82.8	17.0	36.4	46.6
Waubesa	1.0474	0.1323	87.4	25.2	34.2	40.6
Kegonsa	1.0705	0.1509	85.9	21.6	31.5	46.9
Wingra	1.0893	0.1893	82.6	15.6	57.9	26.5

In Lake Monona, Twenhofel (1937) reported that the $CaCO_3$ content of the sludge ranges most commonly from 32 to 44%. Loss on ignition (not including the CO_2 of carbonates) was typically between 12 and 14%. Analyses of 6 surface sludge samples when converted to the present basis of calculation yielded Ca-Mg carbonate contents ranging from 29.8 to 45.8% of the dry weight, and organic contents ranging from 15.0 to 16.8%. Hence, the parameters as calculated from losses on ignition agree satisfactorily with calculations based on more exact analyses.

The data for Mendota and Monona in the paper by Black (1929) are somewhat more difficult to interpret, although the Ca-Mg carbonates are of about the magnitude reported above, and the organic carbon converted to simple carbohydrate gives values ranging from 11.8 to 17.6%.

Sawyer *et al.* (1945) analyzed 122 surface mud samples from the 4 large lakes. The organic content of the mud was defined as the difference between the total loss on ignition and the amount of CO_2 taken up by the ash residue in recarbonation. Any water of hydration driven off in the ashing procedure would tend to make the organic content too high and the carbonate content too low. Nevertheless, their determinations of organic matter agree fairly well with those reported here: Mendota (3 samples at 19-24 m water depth)—18.7%; Monona (6 samples at 12 m)—19.5%; Waubesa (6 samples at 7-8 m)—21.8%; Kegonsa (9 samples at 7-8 m)—22.7%.

QUANTITATIVE ASPECTS OF CLADOCERAN REMAINS

In Table IV the total quantities of Cladocera in the sediments are related to 5 parameters of the sediments. Each separate and identifiable skeletal fragment, regardless of how small, was tabulated as an occurrence. Regardless of the basis of comparison used, the four lakes in the Yahara River chain have the same rank order with respect to increasing quantity of Cladocera, namely, Mendota, Monona, Kegonsa, and Waubesa. Wingra usually comes between Monona and Kegonsa, although on the basis of "residue" (= silica, chiefly) it comes between Kegonsa and Waubesa. This is also the same rank order of increasing organic content of the sediments (Table III), except for the relatively low content in Wingra.

The quantity of cladoceran remains in the sediments tends to follow the general levels of standing crops of plankton in the lakes, and hence can reasonably be used in paleolimnological studies as a rough indication of past primary production. Birge and Juday (1922) worked most intensively on Mendota and Monona, less extensively on Waubesa, and made only one observation on Kegonsa. The average dry weight of net plankton per liter was 0.491 mg for Mendota, 1.414 for Monona, 2.182 for Waubesa, and 6.112 for Kegonsa. The average dry weight of nannoplankton was 3.090 mg for Mendota, 4.433 for Monona, and 5.665 for Waubesa. During May-November of 1939 the dry weight of total plankton varied from 2.32-6.50 mg per liter in Monona, 3.54-21.29 in Waubesa, and 1.79-25.75 in Kegonsa (Frey 1940). The standing crop in Waubesa was quite consistently higher than in Kegonsa. The aver-

TABLE IV. Quantitative aspects of the cladoceran remains in the sediments of the Madison lakes, based in each case on the complete examination of 1/75 cc of fresh sediment. Morphometric data for the first 4 lakes are from Juday (1914), those for Wingra are from Pearse and Achtenberg (1920)

Lake	Area (km²)	DEPTH (m)		PERCENTAGE COMPOSITION					Total remains in 1/75 cc wet sediment	THOUSANDS OF REMAINS PER GRAM			
		Max.	Mean	*Daphnia*	*Bosmina*	*Chydorus sphaericus*	Other chydorids	Other cladocera[1]		Dry wt.	Ash wt. 550°	Loss on ignition (550°)	Ash wt. 550° minus calc. $CaCO_3$
Mendota	39.40	25.6	12.1	16.3	3.3	43.8	36.6	0	153	53	62	352	124
Monona	14.10	22.5	8.4	13.3	5.2	67.8	13.1	0.6	345	137	165	809	294
Waubesa	8.24	11.1	4.9	6.2	16.9	55.6	20.9	0.4	487	276	369	1097	680
Kegonsa	12.73	9.6	4.6	5.4	8.5	65.4	20.2	0.7	461	229	292	1061	488
Wingra	0.81	4.3	1.6	1.2	42.9	22.7	33.2	0	410	162	192	1042	613

[1] *Sida, Latona, Ceriodaphnia, Leptodora.*

age standing crop of net zooplankton (rotifers, copepods, and Cladocera) during this same year were 204 per liter for Monona, 413 for Waubesa, and 277 for Kegonsa. Domogalla (1935) reported on the number of net phytoplankton per liter for the summer months of 1925 and 1935. In 1925 Mendota was lowest and Waubesa the highest; in 1935 Monona was the lowest (presumably as a result of treatment with $CuSO_4$) and Waubesa the highest. Domogalla and Fred (1926) studied the organic nitrogen content (soluble and insoluble) of the lake waters from March-December 1925. The mean values as mg/L calculated from their Table 2 are: Mendota 0.881, Monona 0.936, Waubesa 1.100, Kegonsa 1.032, and Wingra 0.768. Mendota was observed to have the least amount of phytoplankton and Waubesa the most.

The low value of organic nitrogen for Wingra is explained in part by the small amount of soluble organic nitrogen flowing into the lake, and by the protected nature of the lake which would permit the particulate organic nitrogen to settle more rapidly to the bottom. Tressler and Domogalla (1931) described the composition of the plankton and the seasonal development of the various species in Wingra but they did not give any data on numbers or weights. They noted that bluegreen algae were never so abundant here as in the other Madison lakes. However, Sawyer *et al.* (1945) found that Wingra was the heaviest producer of bluegreens, although these seldom reached a nuisance level. Because mean sizes of standing crops were not discussed, it is not certain from this paper where Wingra fits into the rank order of plankton production, except that it is in the same general level as Monona and Kengosa. Waubesa was consistently the richest of the 5 lakes in number of blooms, number of species represented at any one time, and average plankton volume.

The various studies are in agreement that for the 4 lakes in the Yahara River channel, Waubesa has the highest standing crop of plankton, followed by Kegonsa, Monona, and Mendota. This is exactly the rank order of the cladoceran remains in the sediments. The standing crop of plankton in Wingra is greater than Mendota but less than Waubesa, and hence it, too, falls into the same general sequence shown in Table IV.

There is an inverse relationship between size of these lakes and their mean depth and the quantity of cladoceran remains in the sediments. Rawson (1955) has already demonstrated a similar relationship in larger lakes for the standing crops of plankton and benthos and for fish production. Such relationships might not be expected to hold in the Madison lakes because of the heavy fertilization Monona, Waubesa, and Kegonsa have received from treated sewage effluent, and also because of $CuCO_4$ treatment to control algae, which has been practised in Monona since 1918 and in the other 2 lakes since 1935 (Lackey and Sawyer 1945). At the time of their survey Sawyer *et al.* (1945) pointed out that Waubesa was the most heavily fertilized lake, Kegonsa next, followed by Monona, and Mendota. Wingra was somewhat of an anomaly in that it maintained high levels of production without any appreciable amounts of pollution contributing to the nutrient supply.

Although the numbers of cladoceran remains in the sediments of the Madison lakes are large, they are not the largest reported in the literature. In Linsley Pond, Connecticut, *Bosmina* reached a maximum of 67,400 per cc of sediment and somewhat more than 800,000 per gram inorganic matter (Deevey 1942). Quantitative counts of the other Cladocera were not made. In the Upper

Swamp Deposit of Pyramid Valley, New Zealand, Deevey (1955) found a maximum of about 18,000 Cladocera per cc, chiefly *Pleuroxus hastirostris.* In Lake Galichskoye, Russia, Korde and Ulomskii (1959) obtained a maximum of 22,650 remains per cc, representing more than 11 species of Cladocera. The greatest populations reported to date, however, are in Schleinsee in southern Germany, where the number of *Bosmina* per gram ash weight (at 550°) ranged from 1.7 to 22.2 million (up to 440,000 per cc of fresh sediment) and of chydorids and *Sida* from 0.9 to 4.5 million (Frey 1960a).

PERCENTAGE COMPOSITION OF MICROFOSSIL POPULATION

The percentage composition of the cladoceran remains in the sediments (Table IV) is interesting. In the first place, unlike Linsley Pond (Deevey 1942), Windermere (Scourfield 1943), and Schleinsee (Frey 1960), in which *Bosmina* is by far the most abundant cladoceran in the sediments, *Chydorus sphaericus* is dominant in the 4 large Madison lakes, and even in Wingra this species comprises almost one-fourth of the total population. Of the many species of chydorids, *C. sphaericus* is the only one that commonly occurs in the plankton (Rylov 1935). Birge (1898) regarded *sphaericus* as a littoral form that gets into the plankton by accident and maintains itself there as long as suitable food is present. In Mendota the abundance of *sphaericus* seemed positively correlated with *Anabaena,* which, along with other bluegreen algae, Birge assumed to be the main food of this species. Whatever the controlling factors are, *C. sphaericus* is abundant in the plankton of the Madison lakes, typically reaching its population peak in late summer or early autumn. Thus, Birge (1898) reported maxima of 279,000/m^2 of lake surface in 1894, 163,000/m^2 in 1895, and 748,000/m^2 in 1896. These populations maxima would represent densities between 64 and 292 or 135 and 619 organisms per liter, depending on whether Birge's calculations were based on maximum depth or mean depth, presumably the latter. In 1939 the mean population densities of *C. sphaericus* were 39 organisms per liter in Monona, 109 in Waubesa, and 48 in Kegonsa (Table V). The maximum density was 1012 organisms per liter in Waubesa on July 6 at a depth of 2 m. Tressler and Domogalla (1931) found *sphaericus* present in the plankton of Wingra from mid-April through December, with a major peak in late May and a lesser peak in October. The May peak was greater than any pulse of *Daphnia* or *Bosmina.* Thus *C. sphaericus* is definitely an important component of the plankton of the Madison lakes, and because of its small size it might be expected to have a more rapid development and therefore to contribute more exuviae to the sediment than larger plankters such as *Daphnia.*

For the other components of the sediment population there are some progressive changes that seem to be related to the morphometry of the lakes. Thus as the area and mean depth decrease, *Daphnia* becomes relatively less abundant, whereas *Bosmina* and chydorids other than *C. sphaericus* increase. The 2 exceptions to these trends are for *Bosmina* in Kegonsa and other chydorids in Mendota. Table V indicates that the lower value for *Bosmina* in Kegonsa relative to Waubesa is probably real. At present there is no explanation for this.

The high value for "other chydorids" in Mendota is at least partly artificial, in that the exuvial components were more highly fragmented in this lake than in any of the others (which may be related to the much higher populations of offshore benthos in this lake, as described by Frey 1940 and Sawyer *et al.* 1945), so that each individual exuvia in Mendota has the chance of being represented by more fragments in the sediments. Needless to say, most of these fragments were so small that the morphological details were insufficient for recognition of species, or even of genus in many instances. Until more conclusive evidence is obtained, Mendota cannot be regarded as being out of place in this series.

TABLE V. Mean population levels of plankton Cladocera in Madison lakes in 1939 (previously unpublished data collected by Frey)

Lake	Inclusive sampling dates	No. samples	ORGANISMS PER LITER					
			Daphnia	*Diaphanosoma*	*Bosmina*	*Chydorus sphaericus*	*Leptodora*	Totals
Monona..........	June 21-Oct. 2	10	27.2	—	0.2	38.8	—	66.2
Waubesa.........	May 5-Nov. 14	36	52.6	7.9	11.3	108.8	—	180.6
Kegonsa..........	May 5-Nov. 14	37	23.8	5.0	2.1	47.9	0.4	79.2

The percentage composition of the remains in the sediments is roughly related to the relative abundance of the organisms in the plankton. Closer comparison is difficult, because each individual contributes an exuvia for each instar in its development, and the number of instars can vary greatly from family to family and individual to individual. Moreover, preservation of the components of the exuviae varies tremendously.

In *Daphnia* only the postabdominal claws, sometimes with postabdominal teeth attached, were found in the quantitative preparations. Hence, each occurrence represents an instar of an individual. Since nearly all the claws were quite large it seems likely there is a differential destruction of claws of early instars, which at least are smaller, making them more difficult to recover quantitatively at scanning magnification (96x).

In *Bosmina* and *Chydorus sphaericus* the dominant remains were head shields and shells. Since these occurred in approximately equal numbers, the total occurrences can be halved to give a more accurate idea of number of contributions from the population.

Too few remains of "other chydorids" were found to determine if the head shields and shells occur in equal numbers. Certainly there is some but not complete duplication. Multiplying the total occurrences by ⅔ might be a reasonable adjustment.

Other Cladocera (*Ceriodaphnia, Leptodora, Latona* and *Sida*) occur mainly as single remains per instar, so that no adjustment of numbers is necessary.

Readjusting the percentage compositions of Table IV on this basis yields the results shown in Table VI, in which *Bosmina* and *Chydorus sphaericus* are reduced relative to the other components. This is probably a more realistic picture of the instar populations than that given in Table IV. To go beyond this requires knowledge of the mean number of instars per individual of the various species, which information is not readily available. Furthermore, it is not yet certain that the early instars are preserved quantitatively as the later instars seem to be.

TABLE VI. Adjusted percentage composition of the cladoceran remains in the sediments, calculated from the data in Table IV: *Daphnia* and other Cladocera x 1, *Bosmina* and *Chydorus sphaericus* x ½, other chydorids x ⅔

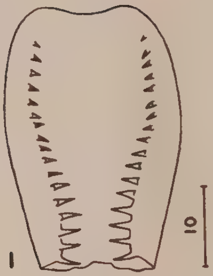
Lake	*Daphnia*	*Bosmina*	*Chydorus sphaericus*	Other chydorids	Other Cladocera
Mendota....	25.3	2.6	34.0	37.9	0
Monona....	22.5	4.4	57.4	14.7	1.0
Waubesa....	10.9	15.0	48.9	24.5	0.7
Kegonsa....	9.5	7.6	57.8	23.9	1.2
Wingra.....	2.1	38.3	20.3	39.4	0

The percentage compositions of the chydorid population as determined from the qualitative and the quantitative slides are given in Table VII. For this comparison the data for all lakes have been combined. In preparing the the qualitative slides Mr. Mueller consciously selected against *Chydorus sphaericus,* but took the others about as they came. Later for each lake an effort was made to pick out remains of the less common species, but these would represent a relatively small fraction of the total.

In spite of the fact that so few specimens are represented in the quantitative material, the agreement between the 2 series is surprisingly close. The

TABLE VII. Comparison of the percentage composition of chydorids in the qualitative and quantitative series from the Madison lakes. The percentages are based on the total recognizable chydorids minus *Chydorus sphaericus,* those for *C. sphaericus* on the total chydorids, and those for unrecognizable chydorids on total chydorids minus *C. sphaericus*

	QUALITATIVE		QUANTITATIVE	
	No.	%	No.	%
Eurycercus lamellatus......	122	4.1	8	3.2
Camptocercus rectirostris...	190	6.4	13	5.2
Camptocercus lilljeborgi....	1	+	—	—
Acroperus harpae.........	213	7.2	10	4.0
Kurzia latissima..........	8	0.3	5	2.0
Oxyurella tenuicaudis......	13	0.4	4	1.6
Graptoleberis testudinaria...	63	2.1	9	3.6
Leydigia leydigi..........	655	22.2	60	23.8
Leydigia acanthocercoides...	11	0.4	—	—
Alona affinis.............	216	7.3	25	9.9
Alona quadrangularis......	794	26.9	48	19.1
Alona rectangula..........	242	8.2	49	19.5
Alona guttata.............	1	+	1	0.4
Alona costata.............	1	+	—	—
Monospilus dispar........	4	0.1	—	—
Alonella exigua...........	12	0.4	2	0.8
Alonella excisa...........	108	3.7	6	2.4
Alonella nana............	1	+	—	—
Alonella rostrata..........	7	0.2	—	—
Dunhevedia crassa........	0	—	—	—
Pleuroxus denticulatus.....	95	3.2	7	2.8
Pleuroxus procurvus.......	50	1.7	3	1.2
Pleuroxus striatus.........	1	+	—	—
Pleuroxus trigonellus......	8	0.3	1	0.4
Pleuroxus aduncus........	111	3.8	1	0.4
Chydorus globosus.........	18	0.6	—	—
Chydorus sphaericus.......	1025	(24.9)	966	(69.2)
Chydorus faviformis.......	4	0.1	—	—
Anchistropus minor.......	1	+	—	—
Unrecognizable chydorids..	137	(4.4)	177	(41.3)
Total chydorids..........	4112		1395	
Total minus *C. sphaericus* and unrecognizable....	2950		252	



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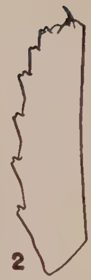

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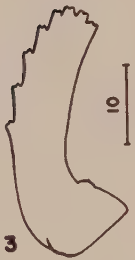
SIDA CRYSTALLINA



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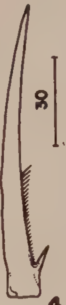
LATONA SETIFERA



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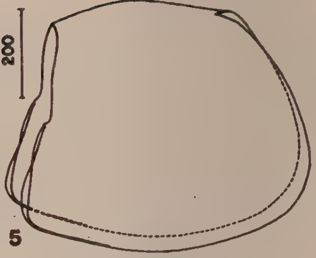

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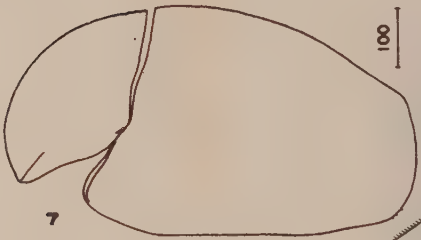
LEYDIGIA LEYDIGI



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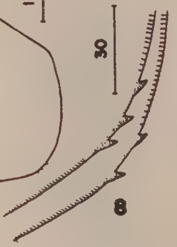

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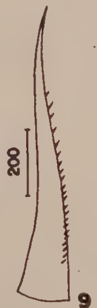
CAMPTOCERCUS RECTIROSTRIS



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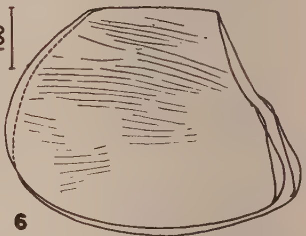
LEPTODORA KINDTI



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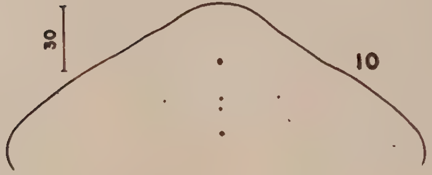

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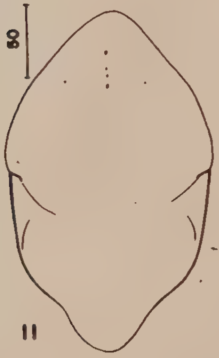

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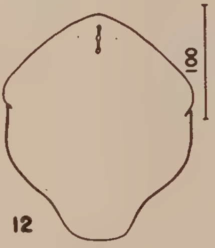

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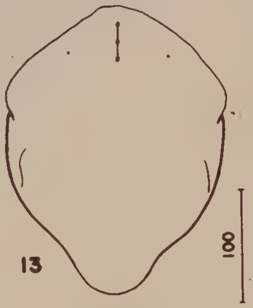
ALONA RECTANGULA

OXYURELLA TENUICAUDIS



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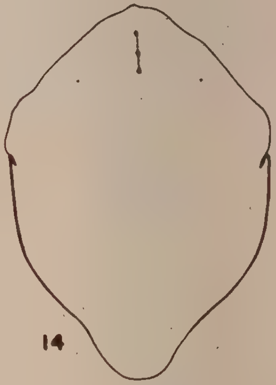

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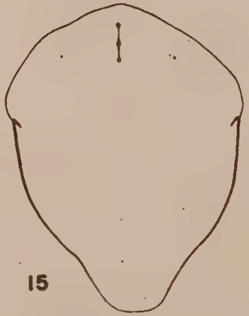

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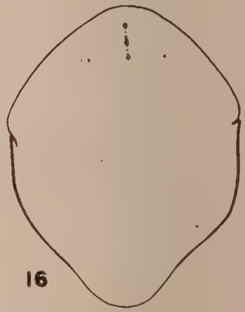

16

OXYURELLA ?

forms with small head shields (*Kurzia, Oxyurella, Graptoleberis,* and *Alona rectangula*) are less well represented in the qualitative series than in the quantitative series, which would be expected. In the qualitative series 25% of the total remains were *C. sphaericus,* whereas in the quantitative series 69% were, showing the degree of selection against this species. Also, in the qualitative series unrecognizable chydorids comprised only 4.4% of the total remains excluding *C. sphaericus,* whereas in the quantitative series they amounted to 41.3%. This again serves to demonstrate the fragmented condition of the remains in the sediments and the consequent difficulty, at least in these lakes, of making a complete quantitative study. However, in such instances a qualitative study can provide a rough approximation of the species composition of the chydorids.

NOTES ON THE VARIOUS SPECIES

Sida crystallina. The distinctive postabdominal claw of this species (Rossolimo 1927: Plate I, Fig. 2) occurs commonly in lake sediments, and has already been reported a number of times. The postabdomen and terminal exopod joint of the antenna are reported here for the first time. The postabdomen (Fig. 1) is readily recognizable by the 2 widely separated rows of spines facing one another. The 3rd exopod segment of the antenna (Fig. 2) has the articular tubercles of 7 swimming hairs, and in addition has 2 spines at the distal end.

Latona setifera remains have not previously been reported from lake sediments. The basal exopod segment of the antenna (Fig. 3) is characterized by an elongated lateral expansion bearing articulation points for swimming hairs.

Daphnia. Two distinct types of postabdominal claws were common in the sediments, and a 3rd type was represented by just a few specimens. The commonest claws had a very large middle pecten, which would most likely make them *D. schødleri* or possibly *D. pulex* (Brooks 1957). A second somewhat less common type with the teeth in all 3 pectens about the same length and stoutness is probably *D. galeata mendotae.* The few specimens in which the teeth of the middle pecten are only slightly longer and stouter than those in the distal pecten are possibly *D. retrocurva.* However, no detailed study has been made of the microfossil remains to determine if these are in fact the species represented.

Ceriodaphnia. Small numbers of postabdominal claws were found in the quantitative preparations, and in the qualitative series there were 2 distinct types of ephippia. No attempt was made to assign these remains to particular species. Birge listed 4 species for the lakes.

Bosmina. No attempt was made to identify the species of *Bosmina* from the head shields and shells in the sediments, although this should be possible with study (Austin 1942). The only 2 postabdominal claws found—one from Waubesa and one from Wingra—were both *B. longirostris.*

Leptodora has previously been recognized in sediments from its characteristic mandibles (Scourfield 1943). Only one mandible fragment was found in the present study, but the spines of the caudal furca (Fig. 9) were relatively abundant. These have not previously been reported.

Camptocercus. The head shields and shells of *C. rectirostris* from the Madison lakes are not completely identical to the populations of Europe. As already reported (Frey 1958, 1959) the head shields of the European species are rounded behind and the shells have a corresponding embayment dorsally to receive this, whereas the head shields of the North American specimens are pointed behind and the shells have a corresponding contour (Fig. 7). Furthermore, the European specimens have fine longitudinal scratch markings between the major longitudinal striae, which the North American specimens appear to lack. Minor differences occur in the denticulation at the posterior-ventral angle of the shell (Fig. 8).

Only a single postabdomen of *C. lilljeborgi* (=*C. macrurus*) was found. Birge noted that this cladoceran was very rare in the Madison lakes. Because of the lack of reference material of *lilljeborgi* it is not now possible

PLATE I[1]

FIG. 1. *Sida crystallina,* postabdomen. Wingra.
FIG. 2. *Sida crystallina,* terminal exopod segment of antenna. Wingra.
FIG. 3. *Latona setifera,* basal exopod segment of antenna. Wingra.
FIG. 4. *Leydigia leydigi,* claw. Wingra.
FIG. 5. *Leydigia leydigi,* shell. Wingra.
FIG. 6. *Leydigia acanthocercoides,* shell. Waubesa.
FIG. 7. *Camptocercus rectirostris,* head and shell. Waubesa.
FIG. 8. *Camptocercus rectirostris,* detail of teeth of same shell. Waubesa.
FIG. 9. *Leptodora kindti,* spine of caudal furca. Monona.
FIG. 10. *Oxyurella tenuicaudis,* detail of head pore arrangement. Pages Lake, N. C. 1948. Mrs. Pamela P. Morford.
FIG. 11. *Oxyurella tenuicaudis,* head shield. Reelfoot Lake, Tenn. 1942. C. C. Hoff.
FIG. 12. *Alona rectangula,* head shield. Monona.
FIG. 13. *Oxyurella* ?, head shield. Mendota.
FIG. 14. *Oxyurella* ?, head shield. Kegonsa.
FIG. 15. *Oxyurella* ?, head shield. Kegonsa.
FIG. 16. *Oxyurella* ?, head shield. Monona.

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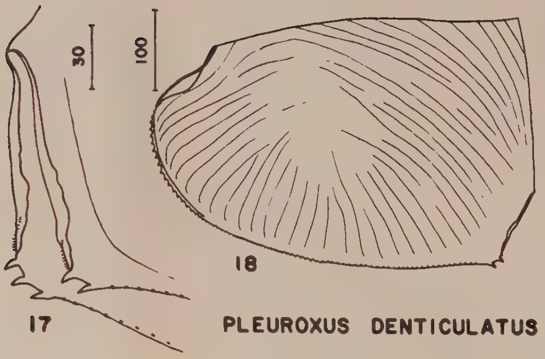
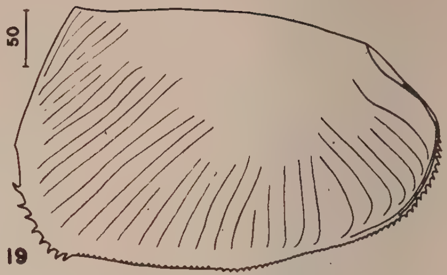
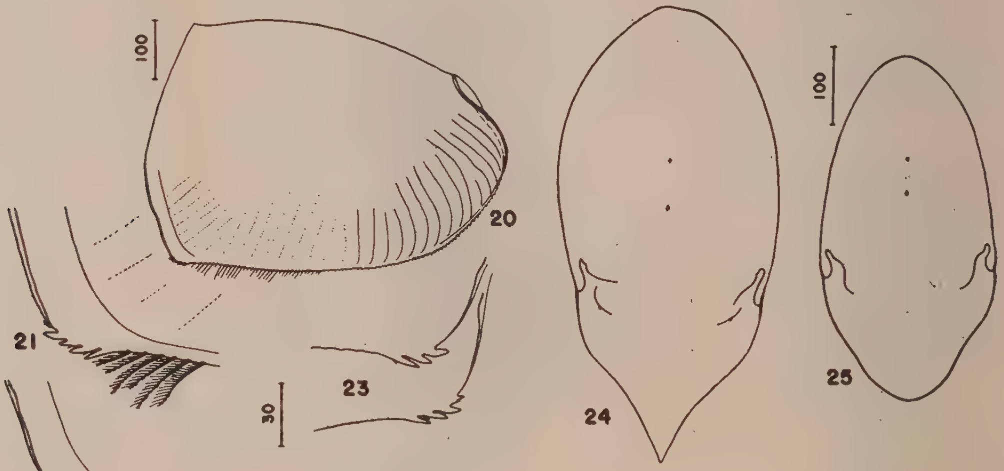
[1] All the figures except the two for *Oxyurella tenuicaudis* have been drawn from microfossils from the Madison lakes by means of camera lucida. The scales are in microns.





PLEUROXUS DENTICULATUS

PLEUROXUS PROCURVUS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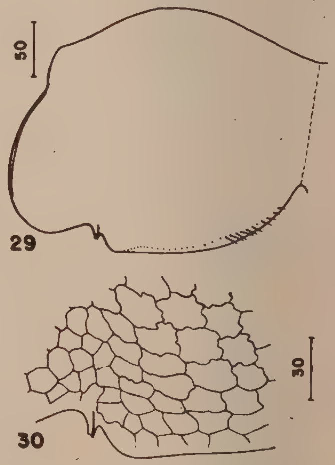
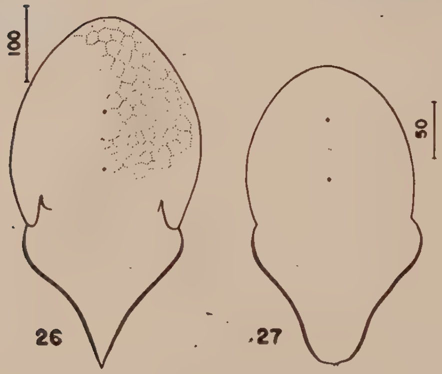
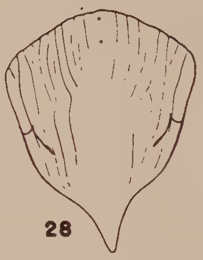
PLEUROXUS ADUNCUS







CHYDORUS SPHAERICUS

ALONELLA ROSTRATA

ANCHISTROPUS MINOR

to distinguish *rectirostris* and *lilljeborgi* on the basis of isolated head shields or shells.

Leydigia leydigi, a very common species in the Madison lakes, has a distinctive head shield with the 3 median pores broadly confluent and the lateral pores closely adjacent (Frey 1959). The head shield is without any surface striae or reticulae. The shell (Fig. 5) has the ventral margin markedly convex, grading into a broadly rounded posterior-ventral angle. The two halves of the shell are separated for a short distance anterior to the distinct posterior-dorsal angle, a feature that seems to be characteristic of the genus (see also Fig. 6).

The caudal claw of this species is long, gradually tapered, and gently curved (Fig. 4). Visible under oil immersion on the concave surface is a series of very fine setae, increasing in length distally. The length of the basal spine is equal to or somewhat less than the basal diameter of the claw. The claws of this species were relatively common in the quantitative preparations.

Leydigia acanthoceroides has the head shield and shell completely covered with very fine striae that are mainly longitudinal, although somewhat swirled in the anterior-ventral quadrant of the shell and along the ecdysial line. In addition, there are relatively coarse longitudinal striae on the shell of the general spacing shown in Figure 6. The shell has the same general shape as that of the previous species.

Oxyurella tenuicaudis. Thirteen head shields from the qualitative slides have been provisionally, although probably erroneously, assigned to this species. The chief characteristic of the head shield of *Oxyurella tenuicaudis* is that the median pores are completely separated from one another without a trace of a connecting channel, and that the middle one of these pores is divided into 2. Moreover, the minor pores, which are relatively large and distinct, are far lateral. This pore arrangement, which has not been observed in any other species of chydorid, is shown in Figures 10 and 11, representing head shields of complete exuviae. The same pore arrangement was observed on one of Lilljeborg's prepared slides, labelled Malmo, 14 August, 1883. On the basis of this information, Figure 111 in Frey (1958) is also of this species.

The head shields from the Madison lakes resemble *Oxyurella* in having the minor pores prominent and far lateral, and in having at least a tendency for the median pores to be isolated from one another. In all specimens there is only a thin chitinous thickening between these pores (Figs. 13, 14, and 15) without any indication of an open channel, and in one specimen the pores are completely separated from each other with two small accessory pores between the three major pores (Fig. 16). The head shields are larger than of *Alona rectangula* (Fig. 12) and the pore arrangement is consistently different.

These head shields may possibly be from *Oxyurella longicauda,* but no reference material is at hand for positive identification.

Alona rectangula is very similar to *A. guttata* in general size and in morphology of head shield and shell (Frey 1958). No certain means of separating these species from fragments is known, except by the postabdomen and postabdominal claws. *A. guttata* is listed here on the basis of one somewhat questionable claw in the quantitative samples, and a distinct var. *tuberculata* shell in the qualitative series. *A. rectangula,* on the other hand, is represented by 7 postabdomens and 6 claws. Hence, without better basis for separation, the head shields and shells of the small Alonas have been tabulated as *rectangula,* which is certainly the most abundant of the 3 small species (including *A. costata* as well).

Alona costata. Only one fragment was found, but this was a head shield with the characteristic transversely elongated minor pores (Frey 1959). No other north temperate *Alona* has been found with such a pore arrangement.

Alona affinis and *A. quadrangularis* are closely related, but can be distingushed readily by the pore arrangement on the head shields (Frey 1959). The caudal claws and postabdomens are likewise quite distinct. The shells are less easy to distinguish, although *affinis* usually has fine, closely spaced longitudinal striae, whereas *quadrangularis* has only coarsely spaced longtitudinal striae. Birge described the population of *quadrangularis* in these lakes as a new species (*A. lepida*), characterized by prominent striae and even reticulae on the shell. The head shield, which also tends to have markings, is typical *quadrangularis* in pore arrangement. Birge noted that this variety was most abundant in Mendota, and this seems to hold for the sediment population as well, as shown in Table II.

Monospilus dispar was found only in Lake Mendota, where it is represented by 4 shells. Although the shells of successive instars do not remain together after KOH treatment as they are in the intact animal, they are readily recognized by the shape of the anterior edge of the shell, and by the ventral border with its characteristic denticles and setae.

PLATE II

FIG. 17. *Pleuroxus denticulatus,* detail of shell. Waubesa.
FIG. 18. *Pleuroxus denticulatus,* shell. Waubesa.
FIG. 19. *Pleuroxus procurvus,* shell. Kengonsa.
FIG. 20. *Pleuroxus aduncus,* shell. Waubesa.
FIG. 21. *Pleuroxus aduncus,* detail of teeth of same specimen. Waubesa.
FIG. 22. *Pleuroxus aduncus,* detail of shell teeth. Waubesa.
FIG. 23. *Pleuroxus aduncus,* detail of shell teeth. Waubesa.
FIG. 24. *Pleuroxus aduncus,* head shield of female. Waubesa.
FIG. 25. *Pleuroxus aduncus,* head shield of male. Waubesa.
FIG. 26. *Chydorus sphaericus,* head shield of large morphological variant with prominent beaded reticulae. The entire head was covered with such markings. Monona.
FIG. 27. *Chydorus sphaericus,* head shield of male. Waubesa.
FIG. 28. *Alonella rostrata,* head shield. Wingra.
FIG. 29. *Anchistropus minor,* shell. Waubesa.
FIG. 30. *Anchistropus minor,* detail of shell showing reticulae. Waubesa.

Alonella exigua and *A. excisa* are readily distignushed by the shape and sculpturing of the head shield (Frey 1959), and by fine striae within the reticulae of the shell of *A. excisa.* However, in small specimens it is often very difficult to distinguish the striae. In such instances the species can be separated by the teeth at the posterior ventral angle, which are strictly terminal in *excisa* and always somewhat subterminal in *exigua.* (Birge 1918: Figs. 1165 and 1166).

Alonella nana is readily recognizable both from its head shield and shell (Frey 1958). The species is recorded in the present study on the basis of a single shell from Wingra.

Alonella rostrata is the species that is called *Rhynchotalona rostrata* in Europe, although it is definitely in the genus *Alonella* (Frey 1959). It is distinct from the species listed by Birge (1918) as *Alonella rostrata,* which must therefore be designated by its prior name *Alonella acutirostris,* as pointed out by Frey (1959). Unfortunately, Brooks (1959) in the new edition of "Fresh-Water Biology" omitted *Alonella rostrata* from the North American fauna. The species is represented in the present material by 3 head shields, 3 shells, and one ephippium. The head shield in Figure 28 is seen to be very similar to that of the European material (Frey 1959: Fig. 48).

Pleuroxus denticulatus shells (Fig. 18) have prominent radial striae, the denticulation along the ventral edge of the shell becomes coarser at the anterior-ventral angle (whence the specific name), and the teeth at the posterior-ventral angle are widely separated and turned downward at their tips (Fig. 17).

Pleuroxus procurvus shells (Fig. 19) are easy to recognize from the series of teeth along the posterior margin, and from the coarser toothing of the shell at the anterior edge, a character this species shares with *P. denticulatus* and *Peracantha truncata.* The head shield is likewise distinct (Frey 1959).

Pleuroxus striatus was abundant in Wingra in late summer and autumn (Birge 1892), but in the present study only a single head fragment was found in Mendota. The characteristics of the head shield are described by Frey (1959).

Pleuroxus trigonellus occurred sparingly although generally. Birge (1892) reported it rather uncommon at Madison, usually occurring in rather deep water, down to 12-15 ft. The head shields and shells can be readily identified (Frey 1958, 1959).

Pleuroxus aduncus is so abundant in Waubesa and Kegonsa it is difficult to see how Birge overlooked it. The shells (Fig. 20) resemble those of *denticulatus* in the pronounced radial striae, which are most distinct in the anterior half of the shell, but the teeth are close together, generally expanded slightly in the middle, turned upward at their tips, and quite variable in number, even in the same individual (Figs. 21, 22, 23). The head shield of the female (Fig. 24) has a shorter rostrum than any other North American *Pleuroxus,* and that of the male (Fig. 25) has an even shorter and broadly rounded rostrum.

Chydorus. All 3 species in the Madison lakes are easy to identify from their head shields and shells (Frey 1958, 1959). The slight emargination at the tip of the rostrum, which is characteristic of *C. sphaericus,* occurs even in the broadly rounded rostrum of the male (Fig. 27). A fair number of head shields of *sphaericus* derive from a large morphological variant characterized by prominent small tubercles along the edges of the reticulae on the shell and head shield (Fig. 26). Within the reticulae are fine, wavy, generally non-anastomosing striae.

Chydorus faviformis, which is so distinctive in appearance because of the deep reticular cells on the head shield and shell, illustrates particularly well how species of low population density can be overlooked even with intensive collecting. This species was found only in Wingra, which is the lake Birge studied most intensively. He described the species the next year (Birge 1893) from northern Wisconsin, where he noticed the distinctive exuviae in the collections before he found any intact specimens.

Anchistropus minor. Birge collected one specimen of *Anchistropus* from Wingra but lost it before the species was determined. In the present study a single shell (Fig. 29) was recovered from Wingra, and this has been assigned to the species Birge later described for North America (Birge 1893). The central portion of the shell has the same type of large reticulae with wavy outlines already illustrated for the head shield (Frey 1959: Fig. 68).

DISCUSSION

The basic raw material of paleolimnology is the sediments that have accumulated in the basin since its origin. From the quantity of these sediments, their physical and chemical composition and the morphological and biochemical microfossils of the plants and animals they contain, deductions are made concerning the past limnology of the basin.

The most abundant microfossils in lake and bog sediments are usually the pollens and spores of terrestrial plants. Botanists have been interested in lake sediments mainly as a vehicle for the chronological preservation of such remains. The major climatic intervals of the region are indicated by changes in the pollen diagram, reflecting associated changes in the vegetation. The presence of prehistoric man can also be detected from changes in the pollen diagrams (*e.g.,* Iversen 1949), and even the influence of early agricultural man on the limnology of lakes (Frey 1955). The paleolimnologist, however, is usually more interested in the pollen diagram as a relative chronology of the site into which the various limnological events and processes can be fitted.

Of the great diversity of organisms in freshwater, relatively few leave morphological remains in the sediments. Sometimes preservation is dependent on particular chemical conditions, as the occurrence of the shells of molluscs and ostracods in calcareous sediments but not in acid organic sediments. Even the preservation of chitinous remains may be markedly affected by chemical conditions, as Krause (1959) has demonstrated.

Among the algae the frustules of diatoms are abundantly represented and can be readily identified to species. Percentage diagrams analogous to pollen diagrams can indicate changes in salinity or temperature in the past (*e.g.,* Florin 1946). Some of the Chlorococcales and desmids are well preserved and can be identified to species, and a few Cyanophyceae can be identified to genus. Korde and Ulomskii (1959, as an example of the type of work done at the Sapropel Institute) have attempted not only to identify the various algal remains to species whenever possible, but also have determined the absolute quantity of the remains in the sediments and correlated these with climatic intervals inferred from pollen diagrams. In general, however, the quantities of planktonic algae, except diatoms, are difficult to determine directly from the sediments. Accordingly, some limnologists are attempting to get an indication of past primary production and of the dominant groups of algae represented from an analysis of chlorophyll derivatives (*e.g.,* Vallentyne 1955) or carotenoids (*e.g.,* Vallentyne 1956) in the sediments.

Morphological remains of animals are just as patchily represented. The testaceous rhizopods have been used to determine periods of relative dryness and wetness in *Sphagnum* bogs (*e.g.,* Grospietsch 1953). The stratigraphic abundance of molluscs and other macroscopic animal remains, and their significance in interpreting the history of lakes has been studied particularly in Russia (*e.g.,* Kozlovskaya 1956). Midge larvae have been especially useful in interpreting the gradual decline in oxygen concentration of the hypolimnion (*e.g.,* Stahl 1959). Recently the oribatid mites in bog sediments have also been studied (Knülle 1957).

Among the zooplankton the copepods and rotifers do not preserve at all, or only under exceptional circumstances (Harding 1956). The Cladocera, however, are well represented, and can occur in tremendous populations comparable to those of pollens and diatoms (Frey 1960a). Accordingly, they seem to offer the greatest promise among the animal remains for giving an insight into past limnological conditions.

At the present level of our knowledge, even the cladoceran record seems patchy. The Sididae, except for *Sida crystallina,* are represented only by antennal segments and mandibles, the Daphnidae by postabdominal claws, mandibles, and ephippia. The Macrothricidae are scarcely ever reported from sediments; possibly their exoskeleton is more subject to attack by bacteria and fungi. The Bosminidae are well represented, and the Chydoridae are represented best of all in terms of species identification. The remaining families are small, with only a species or 2 in each and are of minor importance. However, *Holopedium, Leptodora,* and *Bythotrephes* are known to leave recognizable remains in sediments.

At present only the remains of the Chydoridae can be readily identified to species. This, coupled with their abundance in the sediments, provides a wonderful tool for the study of their present and past zoogeography and their faunal adjustments during the Pleistocene. With further study it may eventually prove possible to identify the sidids and daphnids from their fragments occurring in the sediments, which would considerably broaden the scope and significance of such biogeographic investigations.

For studies of paleolimnology the cladoceran remains promise to be of great significance. Since the total quantity of remains in present-day sediments appears to be quite closely related to mean standing crop of plankton, past plankton production (as indicated by standing crop) can be inferred from the populations of cladoceran remains. Certainly the major changes in abundance of cladoceran microfossils in sediments (Deevey 1942, 1955; Frey 1960a) reflect real changes in plankton production.

The other encouraging aspect of this study is that the composition of the microfossil population seems to bear definite and interpretable relationships to the producing population. Hence, fluctuations in past populations cannot be ascribed to vagaries of preservation but must be responses to changing limnological conditions in the lakes. The interpretation of the significance of these fluctuations is a focal problem of paleolimnology, requiring additional study of the environmental relationships of the various species.

SUMMARY

From a study of the lakes at Madison, Wisconsin, in which the Cladocera are particularly well known, it has been demonstrated that the large accumulation of exoskeletal components in the sediment reflects quite closely the living population as to species present and their relative abundance. Thus, of the chydorids, which are best preserved in the sediments and most easily recognized to species, all the species previously reported were recovered except one, (possibly 2), and in addition 6 not previously reported were found.

By whatever method calculated the 4 major lakes are always arranged in the same rank order with respect to the total population densities of remains in the sediments, indicating real differences in rates of production between the lakes.

Moreover, the mean standing crops of plankton and the quantities of organic nitrogen in the water have the same rank order. Thus, in lieu of data on the phytoplankton itself, the quantities of cladoceran remains in the sediments can be regarded as at least rough indicators of past plankton production.

The precentage composition of the microfossil population appears closely related to that of the producing population, and also appears to be closely related to the morphometry of the lakes. With decreasing area and mean depth in these lakes, *Daphnia* decreases and *Bosmina* increases in relative abundance. Chydorids other than *Chydorus sphaericus,* which is planktonic in the Madison lakes, also increase in relative abundance. Since these latter species are largely substrate organisms occurring in the littoral, their relative increase may be a reflection of the progressive shift in importance from limnetic to littoral production. Similar changes should be found in the ontogeny of individual lakes.

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A COMPARISON OF METHODS FOR CENSUSING WOODPECKERS IN SPRUCE-FIR FORESTS OF COLORADO[1]

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A comparative study of methods for censusing woodpeckers was conducted in the spruce-fir forests of Colorado from October, 1956 to March, 1958 to determine which of the census methods in current use yield the most reliable estimates of woodpecker population densities. The benefits sought from this study were to aid population research on woodpeckers and to facilitate a more accurate appraisal of the role of these birds in biological control of the Engelmann spruce beetle (*Dendroctonus engelmanni* Hopkins). This project was coordinated with ecological research in progress on woodpeckers of the Rocky Mountain area (Baldwin 1960).

Several previous studies of bird censusing techniques were helpful in this investigation. Kendeigh (1944) describes the method of taking a breeding bird census in which a plot is selected and parallel cruise lines traversing it are established. The route taken during the census can be along the lines or between them. This method was used in the present study, since it was felt that it would give a complete survey of the area, thus making it possible to count nearly all the woodpeckers. A census of the entire area would provide a figure for number of birds per acre against which could be compared the results of other methods.

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Twomey (1945) used sample plots 30 meters square in censusing the bird population of an elm-maple forest. Turček (1949) used plots of one hectare (approximately 2.5 acres) as an index to bird populations in forests of South Slovakia. Yeager (1955) employed circular quarter-acre plots, 120 feet in diameter, to determine woodpecker populations in spruce-fir forests of Colorado.

Several methods involving variable-width strips based on the behavior or conspicuousness of birds have been devised. Fisher (1939) used the King method to census eastern ruffed grouse. The average flushing distance of grouse was used to represent one-half the width of the strip censused. Kendeigh (1944) reported a similar method for small birds based on the distances at which a particular species first attracted his attention. The average of these distances was also used to represent one half the width of strip counted. Hayne (1949) devised a method using the flushing distances to determine the numbers of pheasants or grouse in an area. All birds flushed at one distance were used in computing the number of birds per acre using the flushing distance as one half the width of strip censused. This was done for each class of flushing distance and group of birds flushed at that distance. The data derived in this manner were added to give total population.

STUDY AREAS

It was decided to test several census methods for differing population levels of woodpeckers. The abundance of woodpeckers hinged on the availability of bark beetles, mainly the Engelmann spruce beetle and secondary bark beetles associated with it.

The east side of Wolf Creek Pass, at an elevation of 10,500 feet, suffered a severe outbreak of the Engelmann spruce beetle in 1956 and was selected as the first area for study. This area had an eastern exposure with moderate slope and dominant vegetation consisting of Engelmann spruce (*Picea engelmanni*) and sub-alpine fir (*Abies lasiocarpa*).

The second area chosen for study, at Hidden Valley in Rocky Mountain National Park at an elevation of 9,500 feet, had an endemic population of Engelmann spruce beetles. This area had a northern exposure with a steep slope. Trees found here were Engelmann spruce, sub-alpine fir, lodgepole pine (*Pinus contorta*) and limber pine (*P. flexilis*). These were nearly all living trees.

The third area was selected at Rabbit Ears Pass in Northern Colorado at 9,500 feet elevation. An epidemic of the Engelmann spruce beetle had occurred in this area between 1948 and 1951, and much standing dead timber was still present though the beetles were at an endemic level. Engelmann spruce, sub-alpine fir, and lodgepole pine were the principal tree species at this location.

WOODPECKER ACTIVITY

Three species of woodpeckers known to feed on the Engelmann spruce beetle (Hutchison 1952) were censused. These were the Hairy Woodpecker (*Dendrocopos villosus*), the Downy Woodpecker (*D. pubescens*), and the Northern Three-toed Woodpecker (*Picoides tridactylus*).

In good weather, feeding activity was greatest in the early morning soon after dawn and again in late afternoon. Feeding activity appeared to be reduced and concentrated in mid-day during adverse periods. No variation in feeding activity could be attributed to temperature, which varied from 8° to 23°F in the mornings and from 10° to 27°F in the late afternoons.

Woodpeckers apparently were influenced little, if at all, by activities of the census taker. Most birds could be approached as closely as 10 to 20 feet while they were feeding on the lower boles of trees. When they were higher it was possible to walk directly beneath the tree without disturbing them. The counting procedures were based on the feeding activity of the birds. In most cases, it was necessary to hear the bird before it could be located because of the density of the forest and the habit of the woodpeckers of remaining on one tree for a considerable period of time while feeding.

METHODS

Census

In each of the areas, one 20-acre plot was arbitrarily selected to represent typical Engelmann spruce beetle infestation in the area. The study plots were of different shapes because of irregularities in terrain and plant communities. The plot at Wolf Creek Pass was 8 by 25 chains, the plot at Hidden Valley was 10 by 20 chains, and that at Rabbit Ears Pass was 6 by 33.5 chains. Parallel cruise lines traversing the length of each plot were established at 2-chain intervals. Trees were marked along the cruise lines at one-chain intervals so they could be easily followed. The outside boundaries of the plots were not marked, since the methods employed required judging specific distances on each side of the cruise lines. This type of plot, with measured boundaries and traverse lines, is referred to below as the fixed plot.

When censusing by the fixed-plot method (method 1) the cruise lines were followed, and stops of 10 to 15 seconds were made each half chain to listen for woodpeckers. All woodpeckers heard within one chain of each side of the cruise lines were counted. In case of doubt, the distance was paced at a right angle from the line to the tree in which the bird was located. The entire 20-acre plot was covered by this method.

Two methods involving small sample plots were also tested. The one-acre method (method 2a) utilized 10 samples (2 by 5 chains) or a total of 10 acres selected systematically from fixed-plot data. The selection of one-acre units from the fixed-plot data was possible, since fixed-plot censuses were summarized at the end of each acre. The first acre from each fixed-plot census was selected at random and every other acre thereafter was used for the one-acre method.

The 2nd sample-plot method (method 2b) used quarter-acre plots and was devised by Yeager (1955). In the present study, each census usually consisted of 10, quarter-acre samples. However, this varied from 9 to 20 samples, or an 11 to 25% survey. A 5-minute listening period was spent on each quarter acre, providing ample time to locate and identify woodpeckers. The quarter-acre censuses were made on the fixed plot independently of the regular fixed-plot counts.

Strip sampling methods were tested by means of simultaneous counts. The data were collected by recording all woodpeckers detected and their distances at a right angle to the cruise line. This counting procedure was used for 2 independent series of data, one series of counts being taken along the cruise lines of the fixed plot and the other along a narrow logging road which passed through the plot. This permitted computing numbers of birds per acre for each strip method from the same data and minimized variability due to days, time of day, weather conditions, and behavior of the woodpeckers.

One fixed-width-strip method (method 3) was tested employing a strip 66 feet wide, 33 feet on each side of the cruise lines, and giving a 50% survey of the fixed plot.

Five variable-width-strip methods were also tested with the simultaneous data. The first of these (method 4a) used a width of strip based on the average of the greatest distances of all species of woodpeckers from the cruise line, taking this as one half the width of strip censused. The 2nd (method 4b) utilized the greatest distance at which each species was heard to determine one half the width of strip censused, and the number of each species of woodpecker per acre was computed separately. The 3 figures were then added to give total number of birds per acre.

The 3rd variable-width-strip method (method 4c) used the average distance that individuals of each species were observed from the cruise line as one half the width of strip censused. The total number of birds per acre was derived by adding the separate estimates of the 3 species of woodpeckers censused. The 4th (method 4d) was a modification of King's method. The average distance of all species at a right angle from the tree to the road or cruise line was used, rather than flushing distance at any angle, in determining the width of strip censused. The 5th (method 4e) was the method of Hayne (1949) with one modification: the distances birds were located at a right angle from the road or cruise line were used, rather than flushing distances, for computing the width of strip for each group of birds observed in the same distance class.

Analytical Procedures

The number of birds per acre was computed by dividing the number of birds counted by the number of acres censused. An analysis of variance of these figures was then made to determine whether the results in mean birds per acre obtained by any one method were significantly different from those acquired by other methods.

It may be questioned whether it is appropriate to use the analysis of variance tests for the bird census data, because of probable heterogeneity of variances and lack of normal distribution. However, we are advised by E. E. Remmenga (personal communication) that, according to Chebysheff's inequality (Dixon and Massey 1957), the error is limited. Where the analysis of variance indicates significant differences among the means at the 95% level, defects in the data would not lower the level of significance below 89%. Since it is impractical to gather sufficient field data to eliminate defects, one may accept this loss as a practical and still useful solution. Another solution is to eliminate defects by statistical transformation of the data, but this is a time-consuming

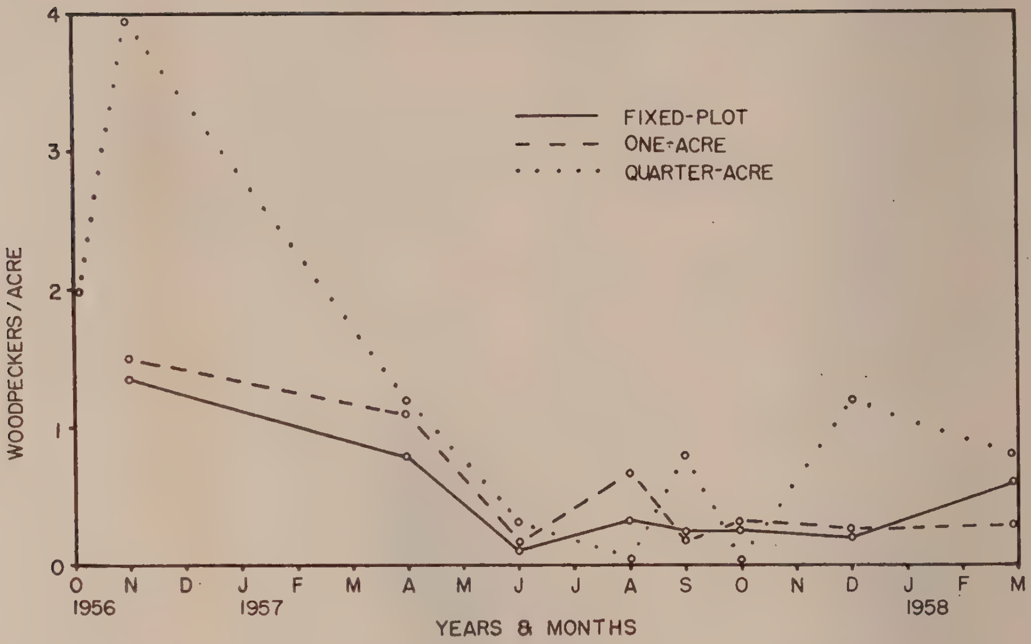

FIG. 1. Numbers of woodpeckers recorded by 3 methods at Wolf Creek Pass.

and expensive procedure which usually could not be justified by the small increases in accuracy achieved.

To reduce the effect of zero counts, data used in making an analysis of variance of the results obtained by the fixed-plot method (1), one-acre method (2a), and quarter-acre method (2b) were taken on days when woodpeckers were counted with all 3 methods. In addition, whenever all methods were not used on the same day, counts taken on the day preceding or following were used. Owing to the small number of woodpeckers counted in the low populations on the plots at Hidden Valley and Rabbit Ears Pass, comparisons of means by analysis of variance were confined to results obtained at Wolf Creek Pass.

RESULTS

The average number of woodpeckers per acre for the 18 censuses[3] taken by the fixed-plot method (1) at Wolf Creek Pass was 0.30. Seven censuses by this method at Hidden Valley gave an average of 0.20 birds per acre and 2 zero counts. The average for 7 counts at Rabbit Ears Pass was 0.06 birds per acre with 5 zero counts.

The one-acre method (2a) gave an average of 0.34 woodpeckers per acre for 18 censuses[3] a Wolf Creek Pass, with 4 zero counts. An average of 0.09 birds per acre with 2 zero counts was recorded for 7 counts by this method at Hidden Valley. No woodpeckers were recorded at Rabbit Ears Pass during the 7 counts by this method.

The quarter-acre method (2b) gave an average of 0.73 birds per acre for the 15 censuses[4] taken at Wolf Creek Pass. No woodpeckers were recorded at Hidden Valley during the 2 times this method was used nor at Rabbit Ears Pass where it was used 3 times. Notwithstanding, woodpeckers were present on both days the quarter-acre method was used at Hidden Valley and during 2 of the days at Rabbit Ears Pass. After applying the quarter-acre method at 11-25% coverage on the 3 plots, results were found to be more erratic than those from the other methods. To increase the effectiveness of the quarter-acre method would demand much higher coverage, especially where woodpecker populations were low. Because of time limitations, the method was discontinued in the latter 2 areas.

Results of these 3 methods are shown in Figures 1 and 2. Since several censuses were taken during some months (see footnotes 3 and 4), these data represent the greatest number of woodpeckers recorded for one census during the month.

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[3] Number of counts for each month: Nov. 1956, 1; Apr. 1957, 2; June 2; Aug. 3; Sept. 4; Oct. 2; Dec. 3; Mar. 1958, 1.

[4] Number of counts for each month: Oct. 1956, 1; Nov. 1; Apr. 1957, 2; June 1; Aug. 1; Sept. 2; Oct. 2; Dec. 4; Mar. 1958, 1.

The analysis of variance for the data from Wolf Creek Pass showed that numbers of birds per acre obtained by the 3 methods did not differ significantly at the 5% level (Table I).

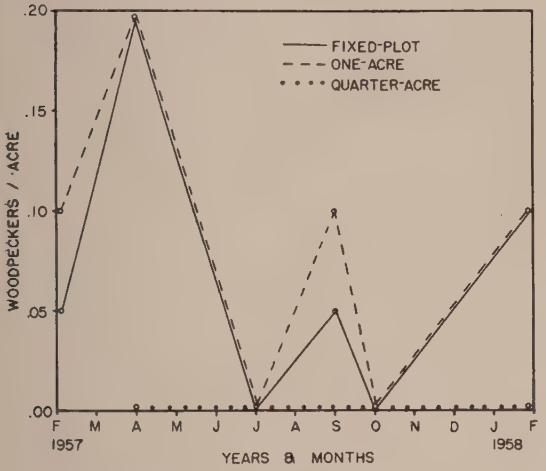

FIG. 2. Numbers of woodpeckers recorded by 3 methods at Hidden Valley.

TABLE I. Analysis of variance of mean woodpeckers per acre recorded by the fixed-plot method, one-acre method, and quarter-acre method at Wolf Creek Pass

Source of variation	Degrees of freedom	Means of squares	Observed F
Methods	2	1.15	3.29
Days	5	1.74	4.95*
Error	10	0.35	

* Significant at the five per cent level.

Variable-width-strip methods (4a-4e) were first tested using data from 22 censuses[5] made along the narrow road extending through the heavily infested end of the 20-acre plot at Wolf Creek Pass. The results obtained from this comparison are shown in Figure 3. The number of counts yielding particular values for woodpeckers per acre is indicated by height of the bars, while the mean value of woodpeckers per acre is shown separately in each box. The first 2 methods (4a and 4b) of computation, employing average greatest distance of all species and greatest distances of each species separately to determine width of strip censused, gave means of 1.91 and 2.07 woodpeckers per acre, respectively. These 2 methods and Hayne's (4e) use the largest areas in computing birds per acre. The 3rd and 4th methods (4c and 4d), computing width on the basis of average distance of each species separately and average distance of all species, gave means of 3.13 and 2.84. The areas used in these latter methods are smaller. The 5th method (4e), Hayne's modified, which uses the same area as the 2nd method (4b) and also in effect enlarges the number of birds used in the computations, showed a mean of 5.01 woodpeckers per acre. This last method results in distinctly higher figures for birds per acre. The spread of the bars to the right in Fig. 3 indicates the relative magnifying effect for each method.

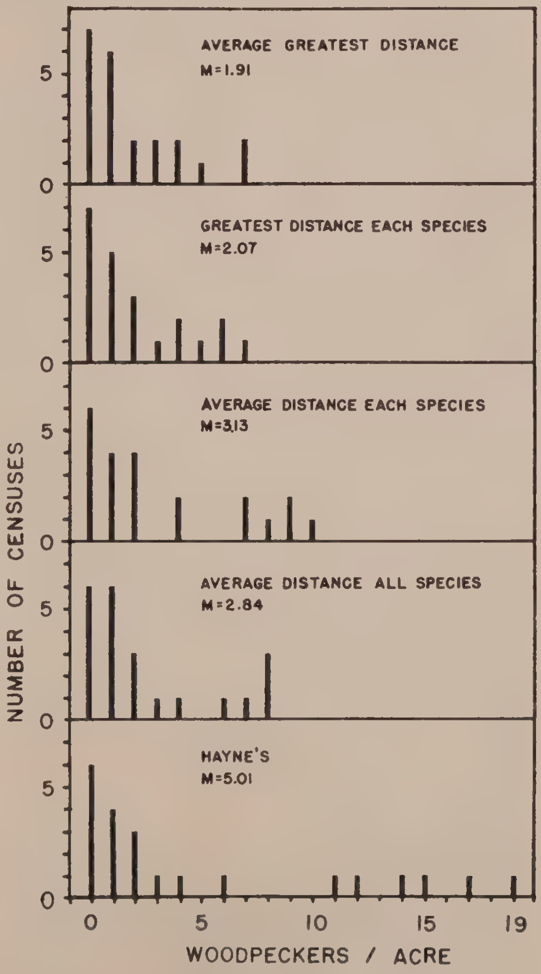

FIG. 3. Variation in results of variable-width-strip methods.

The 2nd test of variable-width-strip methods, made with simultaneous data from the fixed plot at Wolf Creek Pass, gave results presented in Table II. The 2 greatest-distance methods (4a and 4b) gave the lowest means, the 2 average-distance methods (4c and 4d) gave intermediate values, and Hayne's method (4e) gave the highest

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[5] Number of counts for each month: Oct. 1956, 4; Nov. 3; Apr. 1957, 5; June 2; Aug. 2; Dec. 6.

TABLE II. Numbers of woodpeckers obtained by 7 methods in simultaneous censuses on the fixed plot at Wolf Creek Pass

Date	Fixed plot	Fixed width strip	Average greatest distance all species	Greatest distance each species	Average distance each species	Average distance all species	Hayne's method
10-11-57	0.05	0.00	0.07	0.07	0.07	0.07	0.07
10-12-57	0.25	0.20	0.17	0.17	0.31	0.31	0.46
12-18-57	0.10	0.10	0.18	0.11	0.28	0.18	0.28
12-19-57	0.20	0.30	0.26	0.13	0.54	0.33	0.93
3-18-58	0.60	0.80	0.60	0.60	1.33	1.33	2.23
Totals. . . .	1.20	1.40	1.28	1.08	2.53	2.22	3.97
Means. . . .	0.24	0.28	0.26	0.22	0.51	0.44	0.79

L. S. D. 95% level = 0.40.

mean, so the results in the 2nd test confirm those of the first test as to relative magnification of the 5 methods. However, because of size of sample, the data obtained along the road should give the more accurate comparison.

Analyses of variance made to compare the mean numbers of woodpeckers per acre obtained by the 5 variable-width-strip methods (4a-4e) showed differences among means of the first test to be significant at the one % level (Table III). Differences among means of the 2nd test were significant at the 5% level (Table IV). Although the analyses of variance indicate that the methods give different results, they do not tell which of the 5 methods are most accurate.

TABLE III. Analysis of variance of mean woodpeckers per acre computed by 5 variable-width-strip methods from data obtained along the road at Wolf Creek Pass

Source of variation	Degrees of freedom	Means of squares	Observed F
Methods.	4	33.71	9.56**
Days.	21	56.74	16.09**
Error.	84	3.53	

** Significant at the one % level

TABLE IV. Analysis of variance of mean woodpeckers per acre obtained by 7 methods in simultaneous censuses on the fixed plot at Wolf Creek Pass

Source of variation	Degrees of freedom	Means of squares	Observed F
Methods.	6	0.21	3.59*
Days.	4	1.12	18.33**
Error.	24	0.06	

* Significant at the 5% level.
** Significant at the one % level.

To locate the means which are significantly different, we may use the least significant difference as an aid. The least significant difference at the 95% level of 0.16 for means of the first test suggests that all variable-width-strip methods produced different results. The least significant difference of 0.40 for the means of the 2nd test, however, indicates that Hayne's method (4e) gave results significantly larger than all other methods, including fixed-plot (1) and fixed-width-strip (3), tested in the simultaneous counts, except the 2 average-distance methods (4c and 4d). All methods other than Hayne's (4e) employed in the 2nd test gave numbers of woodpeckers per acre which did not differ significantly.

The method giving results most closely paralleling those of the fixed-plot method (1) can be considered the most accurate, since this method covered the entire 20-acre plot and recorded nearly all woodpeckers present. The 2 greatest-distance methods (4a and 4b) gave results equally close to those of the fixed-plot method (1).

DISCUSSION

Field Operation

The fixed-plot (1) requires considerable time to mark the cruise lines. All of the other methods used in this study require no advance preparation. However, the latter methods require keeping a straight line with a hand compass and pacing the length of the strip censused or the distance between samples and length of samples. These operations tend to detract attention from the actual counting.

Completeness of Count

The fixed-plot method (1) was not strictly a sampling scheme in that it covered the entire 20 acres and presumably recorded all woodpeckers present. Other methods were tested at coverages from 11 to 100%. The percentage of coverage tends to be fixed partly by characteristics of the individual methods and, as in the methods of low coverage in this study, partly by limitations on time available in the field.

Increases in zero counts resulted with sampling methods which utilized smaller proportions of the sampling areas. This was especially true where woodpeckers were few and sparsely distributed, as at the endemic and past epidemic areas of Engelmann spruce beetle infestation. In using the quarter-acre method (2b), the need for a large number of samples where the population is low involves great disadvantage in the amount of time required to take a census, even when coverage is no higher than 20%. At low population levels, it would be preferable to use a method that gives a high percentage of coverage to increase the chances of counting any woodpeckers present.

The fixed-width-strip method (3) gave good coverage, but the predetermined limit on counting distance prevented the recording of woodpeckers beyond that distance under good conditions. In areas of low woodpecker density the only birds heard may easily be beyond the width of strip being counted, and zero counts are obtained.

The variable-width-strip methods (4a-4e), in which width of strip was based on conspicuousness, gave excellent coverage of the study areas, since the distance at which woodpeckers were heard was often greater than the predetermined 66 feet used as one half the width of strip in the fixed-plot method (1). Also, these methods automatically adjusted the width of strip, correcting for variations in weather factors such as wind which limit the distance woodpeckers can be heard. However, it is suggested that variable-width-strip methods be used only under consistent weather conditions when possible.

Variation in Results

A comparison of the results by analysis of variance of the fixed-plot (1), one-acre (2a), and quarter-acre (2b) methods revealed no significant differences, hence it appeared that no differences developed in numbers of woodpeckers recorded by these 3 methods. However, the mean of the quarter-acre censuses was nearly twice that of either of the other methods, and many more zero counts were recorded. With a larger number of censuses, a significant difference very likely would have resulted. The precision of this sampling procedure would increase with larger samples and also if applied to woodpecker populations of homogeneous distribution.

The analysis of variance and least significant difference between means obtained with 5 variable-width-strip methods (4a-4e) along the road showed that these methods can give very different results. The most divergent results were obtained with Hayne's method modified (4e) and to a lesser extent with the 2 average-distance methods (4c and 4d). These methods tend to correct too highly for birds missed, which, when censusing woodpeckers, are not enough to warrant a correction of such magnitude. The feeding activity of the woodpeckers makes it possible to locate nearly all birds. It is granted that some woodpeckers are missed; however, when the census is conducted at the time of greatest feeding activity (early morning or late afternoon) and under ideal weather conditions (calm and no precipitation) this effect is negligible.

The greatest-distance methods (4a and 4b) appeared to give the most realistic results, and of these 2 the method (4b) using the greatest distance of each species separately to determine width of strip was preferred in this study, because it does not involve a correction of the size that may occur when using the average of the greatest distance of all species. It simply makes allowances for the different distances each species can be heard feeding; for example, the Downy Woodpecker, because of its small size, is not likely to be heard as far as the much larger Hairy Woodpecker. Great error could result in using the method (4b) based on the greatest distance of each species when only one or 2 birds are located, and these by chance are close to the cruise line, even though birds could have been heard for a greater distance had they been present. The counts must be carried on long enough to tally several woodpeckers of each species. In case of very low populations, a census using a strip of predetermined width of possibly 2 chains would tend to be more reliable.

SUMMARY

Nine methods were used between October 1956 and March 1958 to census woodpeckers in 3 areas of spruce-fir forest, each area representing a different classification of Engelmann spruce beetle infestation. These methods were compared on the basis of field operation, completeness of count, and variation in results.

The fixed-plot method (1) with 100% coverage of the study plot was assumed to give the most accurate results and other methods were compared with it.

Results closely comparable to those obtained with the fixed-plot method (1) were produced by the fixed-width-strip method (3) with 33-foot half width of strip, the one-acre method (2a)

with 50% coverage, the variable-width-strip method (4a) using the average of greatest distances of all species for half width of strip, and the variable-width-strip method (4b) using the greatest distance of each species separately for half width.

Extremely variable results, either very high counts or zero counts, were obtained with the quarter-acre method (2b), when applied at 11-25% coverage.

Estimates too large were produced by 3 variable-width-strip methods which corrected for woodpeckers missed, namely, the modification of Hayne's method (4e), the method using average distance of each species separately for half width of strip (4c), and that using average distance of all species for half width (4d).

The method found best for censusing woodpeckers in this study, when employed under consistent weather conditions and with moderately large woodpecker populations, was the variable-width-strip method (4b) utilizing the greatest distance of each species for half the width of strip censused, then adding the three separate population estimates for total population.

ACKNOWLEDGMENTS

Thanks are gratefully extended to Dr. F. B. Knight, Entomologist, Rocky Mountain Forest and Range Experiment Station, U. S. Forest Service, and Dr. E. E. Remmenga, Department of Mathematics, Colorado State University, for their help in the analysis of data and other aspects of the study. The use of equipment and Cooperative Aid funds made available by the Rocky Mountain Forest and Range Experiment Station and support provided by the National Science Foundation are gratefully acknowledged.

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POPULATION ECOLOGY OF WHITE-TAILED DEER IN NORTHEASTERN ALABAMA[1]

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Considerable information has been published regarding the life history and general ecology of the white-tailed deer (*Odocoileus virginianus*) in the northern and western portions of its range, especially in areas where winter yarding and herd formation are prevalent. However, there is a paucity of information from the southeastern portion of the range. Partial explanation for this scarcity lies in the fact that deer were eliminated from most of their southeastern range by the early 1900's and have only recently attained some of their former abundance and distribution through restocking programs.

A program of research into the basic ecology of a white-tailed deer population was initiated in September, 1956 by the Alabama Cooperative Wildlife Research Unit in Auburn, Alabama. Field investigations for this study were conducted on the 40,000-acre Choccolocco Wildlife Management Area, Talladega National Forest, Cleburne County, Alabama, located at a latitude of 33°50′. This region is characterized by an average annual temperature of 61°F and precipitation of 52 inches.

THE STUDY AREA

Physiographically, the Choccolocco Area is a mature, ruggedly-dissected region covered by a mixed pine-hardwood forest. This region represents the southernmost outlier of the Appalachian mountains in Alabama. Most elevations above mean sea level lie beween 1,000 and 1,250 feet with extremes from 850 to 1,700 feet. This mountainous region is peculiar in that it was originally described as a longleaf pine (*Pinus australis*) forest even though it is some distance removed from the extensive longleaf forest belt of the Gulf Coast. The original longleaf dominance has since been replaced by other pines and second-growth hardwoods.

White settlers moved into the Choccolocco Area shortly after the Upper Creek Indians ceded their hunting lands to the United States in 1832 (Owen 1921). As a direct consequence of this area's rugged topography, agricultural practices were limited to small farming operations and logging with minimal adverse effects on wildlife. All families had moved out by 1936 after the U. S. Forest Service acquired the land, and only traces of prior settlement remain today. The U. S. Forest Service, in cooperation with the Alabama Department of Conservation, established the Choccolocco Wildlife Management Area in 1938.

White-tailed deer must have been fairly abundant in the primeval forests of the Choccolocco Area if the Indians burned the woodlands regularly as most authorities believe. It is also likely that deer increased in numbers shortly after settlers moved in and began creating breaks in the canopy with their land-clearing activities. The decline of deer abundance in this region may be traced back to shortly after the Civil War when a major disease distaster is believed to have affected the deer of the southeastern United States (Greer, Shotts and Hayes 1957). A few deer still remained in northern Cleburne County by 1916 (Howell 1921).

Incomplete records indicate that about 65 deer of unknown age and sex were released in the Choccolocco Area between 1938 and 1941. The stocking utilized deer from the Pisgah National Forest descended from a few native animals plus additional deer from the Adirondacks of New York, and from Florida and the coast of North Carolina (Ruff 1938). After stocking, a die-off of major proportions in 1949 decimated the deer population to a very low level, the exact number being unknown. The first managed hunts were conducted in 1948 and have continued uninterrupted through 1958. During this period, 898 legal bucks were removed.

METHODS

The vegetation on the Choccolocco range was surveyed in order to determine its carrying capacity or equilibrium level. This survey was made during the summer of 1957 and winter of 1958 through the use of line-intercepts employing a chain 100 feet in length. To facilitate analysis, this chain was subdivided into 5-foot segments. Since this was a survey of deer range, height of the line was limited to 4½ feet, a figure derived by measuring the maximum, unstrained browsing height of captive deer. In addition to frequency and coverage, degree of browse, canopy composition and site location were recorded.

Range analysis was limited to the 16,000-acre Shoal Creek drainage because it was considered representative of a total area too large to be completely surveyed within the time available. One hundred lines were located at random throughout the drainage by a process of unbiased selection.

Records of deer killed (legal and illegal) since 1953 were utilized in determining physical condition, population composition and rate of change and in obtaining live weights, measurements and reproductive data. All of the deer were aged according to the method described by Severinghaus (1949). Nineteen specimens were collected during the gestation periods of 1957-58-59 to augment reproductive data gathered during the managed hunts.

Complete reproductive tracts were usually preserved; otherwise, only the ovaries and embryos (if present) were retained for further study. Ovaries were sectioned and examined macroscopically for corpora lutea according to the method described by Cheatum (1949). Embryos were measured and aged by the methods of Cheatum and Morton (1946) and Armstrong (1950) and by comparing them with known-age embryos obtained from captive does.

One-quart stomach samples were taken from all specimens collected in addition to 39 ungutted animals brought to the deer checking station by hunters. Analysis was made to determine frequency of occurrence both by season and by total stomachs examined.

Census drives were conducted in November, 1957 and May, 1958 to gain some insight into density and dispersion of deer throughout the Choccolocco Area. In addition, much pertinent information of a general nature was gathered during 190 days of field observation.

RANGE ANALYSIS

Results of the summer and winter range surveys were summarized by cover types applicable to deer usage (Table I). The difference between the summer and winter bare types repre-

Table I. Summary of cover types in the Choccolocco Area as determined by line interception range surveys

	Type Cover	Frequency		Coverage	
		Lines	%	Feet	%
Summer, 1957	Bare	100	100	5,757	57.5
	BARE TOTAL			5,757	57.5
	Grasses	99	99	705	7.1
	Forbs	99	99	772	7.7
	HERBACEOUS TOTAL			1,477	14.8
	Vines	92	92	199	2.0
	Shrubs	100	100	1,888	18.9
	Trees	99	99	679	6.8
	BROWSE TOTAL			2,766	27.7
	VEGETATION TOTAL			4,243	42.5
	TYPE TOTAL			10,000	100.0
Winter, 1958	Bare	50	100	3,867	77.4
	BARE TOTAL			3,867	77.4
	Grasses	34	68	210	4.2
	Forbs	40	80	32	0.6
	HERBACEOUS TOTAL			242	4.8
	Vines	40	80	98	2.0
	Shrubs	48	96	657	13.1
	Trees	44	88	136	2.6
	BROWSE TOTAL			891	17.8
	VEGETATION TOTAL			1,133	22.6
	TYPE TOTAL			5,000	100.0

sented the cumulative difference between the vegetative types during these seasons.

The distribution of forest types in the Choccolocco Area was determined by analysis of canopy composition. Forest types were placed in one of 3 general site categories dependent upon their location on a ridge slope (Figure 1). In essence, the 3 categories of lower, mid and upper ridge position represented decreasing soil moisture.

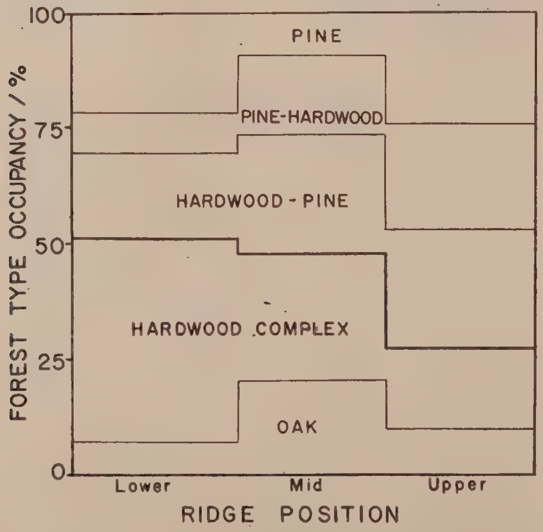

Fig. 1. Distribution of major forest types within the Choccolocco Area by site-moisture relationships.

The summer survey indicated that a wide variety of shrubs and trees were browsed by deer during this period. By far the most important browse species was lowbush blueberry (*Vaccinium vacillans*), which comprised 72% of all shrubs and had 54% of its annual growth utilized. Other heavily utilized browse plants included greenbrier (*Smilax* spp.), hydrangea (*Hydrangea* spp.), strawberry-bush (*Euonymus americanus*), black gum (*Nyssa sylvatica*), mountain laurel (*Kalmia latifolia*), and viburnum (*Viburnum* spp.). As anticipated, the winter survey indicated that deer had less browse available on fewer species of shrubs and trees during this period than during the summer. Greenbrier, hydrangea, dwarf sumac (*Rhus copallina*), mountain laurel, sweetleaf (*Symplocos tinctoria*) and honeysuckle (*Lonicera* spp.) were heavily browsed.

The stomach samples supported the range survey findings with 4 exceptions beyond the limitations of the survey methods employed. These were acorns, fungi, lichens and litter composed of dead plant material which appeared in inverse ratio to the amount of live forage available.

Range Influence

Individual growth of deer and size at maturity are reliable indicators of soil fertility and food quality on any particular range (Taylor 1956). In this respect, the inherent low fertility of the Choccolocco soils and the reduction of the more palatable plant species by prolonged overgrazing have combined to produce deer that are smaller and lighter in weight than would be produced on better range.

Live Weight

Since 1954, a total of 105 live weights was obtained from Choccolocco deer of both sexes and all age groups (Figure 2). A complete separation of the male and female weight-increase curves followed a period of rapid weight gains. This separation coincided with sexual maturity and subsequent pregnancy in females and indicated that this may be a limiting factor in maximum size increase of does.

Antler Development

Prior to 1955, only male deer with branched antlers could be legally harvested by hunters in the Choccolocco Area. This restriction excluded many 1½-year-old deer from the total kill since

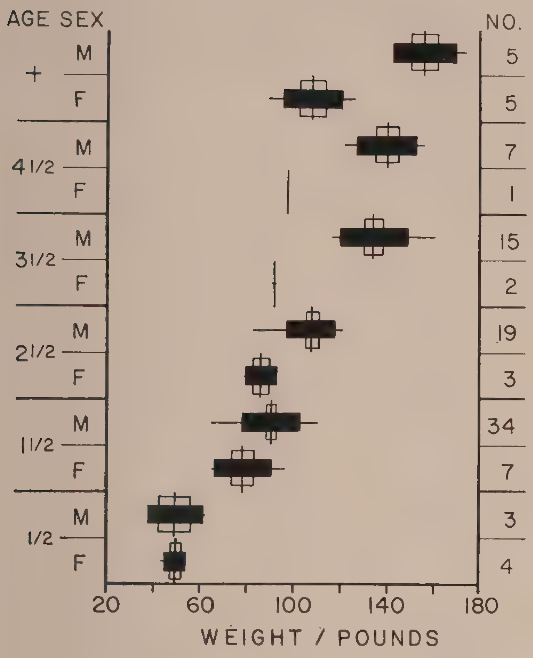

FIG. 2. Variations in live weights of Choccolocco deer by age and sex. Data were obtained from 1954 through 1958. The single vertical line represents the mean, the single horizontal line represents the range, the solid bars represent a total of 2 standard deviations and the open bars represent a total of 2 standard errors.

spike antlers apparently prevailed in this age group. As a consequence, 1½-year-old deer constituted less than 25% of the total kill prior to 1955. Since 1954, visible antlers without regard to branching have been the legal basis for hunting bucks. This change has allowed for greater harvest of 1½-year-old deer (39 to 45% of the total annual kill) than the previous regulation.

Biologically, this has provided an extra means of evaluating trends of range condition. If deer are allowed to exceed range carrying capacity, both qualitative and quantitative food shortages will result. Young deer are the first to feel the effects of food shortage, especially nutritious items. This is reflected in antler development. The increasing number of spike antlers in 1½-year-old Choccolocco deer demonstrated this fact (Table II). The appearance of numerous spikes (at least 35%) in the 2½-year-old group in 1958 further indicated a deterioration of the Choccolocco range as suitable deer habitat.

TABLE II. Percentage of bucks with spikes in the Choccolocco Area—1½ years of age

Year	Percent
1955	76
1956	82
1957	98
1958	96

Eight deer collected in the northern part of the Choccolocco Area during the 1959 gestation period corroborated range survey findings of overbrowsed conditions in this locality. Based on age-weight groups, one deer was one pound above its late fall mean, one equaled its late fall mean and the remaining 6 averaged 16 pounds below their respective late fall means. Outstanding among these departures were a 45 months old doe weighing 65 pounds and a 69 months old doe weighing 77 pounds. Both these does had consumed fresh pine browse in large quantities and were carrying single fawns instead of twins as expected. Even the doe that was one pound above its late fall mean had also ingested some fresh pine browse and was carrying a single fawn although she was probably in her 3rd pregnancy. A single collection was made near the northern boundary of the Choccolocco Area of a 32 months old doe that was also carrying a single fawn despite the probability of the doe being in her 2nd pregnancy.

Coaction of Weather

Climate can influence deer population densities, especially during periods of unfavorable conditions, *i.e.*, overcrowding. Nicholson (1954) stated that climate operating in association with density-governing factors may have a profound influence upon density via properties of animals or environmental favorability.

In addition to the effect of drouth in 1954, field evidence of this coaction was presented during the severe winter of 1957-58. During this period, the most severe winter recorded in Alabama in about 50 years, the nearest weather station in Heflin recorded an average maximum-minimum of 48.6 — 26.0° in January and 49.2 — 24.3° in February. With the possible exception of 3 unrecorded days, no minimum temperatures above freezing were recorded in February on any of 4 maximum-minimum thermometers located in the Choccolocco Area. In addition, a 5-inch snow fell on February 15th and remained on the ground for nearly a week.

Preliminary data indicated that the winter of 1957-58 had a direct influence on the 1958 kill of 1½-year-old deer since proportionally they were not as abundant in relation to 2½-year-olds as they were in 3 previous years (Table III).

TABLE III. Percentage of 1½- to 2½-year-old deer since 1955 when spikes became legal in the Choccolocco Area

Year of Hunt	Number by Age		Total Killed	Percent 1½'s
	1½	2½		
1955	41	21	62	66
1956	54	30	84	64
1957	45	25	70	64
1958	79	74	153	52

Since the 1958 group of 1½-year-olds came into the winter of 1957-58 as 6-month-old fawns, severe weather coupled with food limitations probably would have affected them more than any other age group.

POPULATION DYNAMICS

Unmanaged deer populations tend to regulate their densities in relation to inherent properties and those of the community. This state of balance, however, is constantly oscillating about an equilibrium level or carrying capacity which in turn is forever changing with changing environmental conditions. Nicholson (1954) stated that balance is the corrective movement which opposes each departure from the position of equilibrium. He further stated that the mechanism of density goverance is almost always intraspecific competition for a critically important requisite or limiting factor. Essential to an understanding of the forces producing these changes is an understanding of the extent of predation, composition, distribution and reproduction of the particular deer population under investigation.

Predation

Errington (1946) found that, "Shooting and trapping, in moderation and directed mainly against surpluses, has about the same population role as ordinary predation by native enemies. . . ." According to Nicholson (1954), the role assumed by these "native enemies" or predators is to limit herbivores near the highest level their range can support. In the absence of these predators, however, herbivores reduce their own food to extreme scarcity. With present deer populations, man has replaced these natural predators that were, in most instances, primarily age selective (very young or old) and secondarily sex selective. In contrast to this natural selectivity, man has tended to reverse this situation by being primarily male sex selective through buck laws and secondarily age selective. This reversal has produced many unbalanced populations with more violent oscillations than those exhibited by naturally controlled populations. Thus, it is necessary to include the influence of man, both direct and indirect, in any study of deer populations.

Composition

Comprehensive insight into the composition of the total population was gained in 1958 when, for the first time, a single recorded age group of males was, for all practical purposes, exterminated from the Choccolocco Area. This age group was born in 1952 and represented the 6½-year-old kill of the 1958 hunts. Since no deer were killed over 6½ years of age, it was unlikely that any bucks born in 1952 were left in the population. Assuming this as a known, a total population index was derived by using knowns and proportionalities for the other age groups. This gave a total breeding male production since 1952 of 1,085 deer with 507 remaining (Table IV).

TABLE IV. Male age composition in the Choccolocco Area based on kill data and birth dates

Year of Hunt	Number Killed by Year of Birth						Totals
	1952	1953	1954	1955	1956	1957	
1953	12						
1954	27	23					
1955	13	21	41				
1956	9	28	30	54			
1957	2	13	20	25	45		
1958	2	5	9	36	74	79	
Total killed	65	90	100	115	119	79	578
Estimated remainder	0	10	20	35	111	331	507
Total production	65	100	120	150	230	410	1085

To carry this one step further, does were added to the remaining total. Assuming less mortality and a longer life span, there were an estimated 1,500 breeding does within the population. This produced an approximate sex ratio of 1 male to 3 females and a total breeding population of about 2,000 deer in January, 1959. All factors considered, the 1958 fawn crop was estimated to be 1,500 deer swelling the total population to approximately 3,500 animals.

This information was plotted on semi-logarithmic paper in order better to predict future increases (Figure 3). Of several evident factors, it appeared that the population was undergoing a period of almost unimpeded expansion with the rate of increase near the ecological maximum. Also, the slight depression in population increase in 1954 may be attributed to a severe drouth that occurred that year.

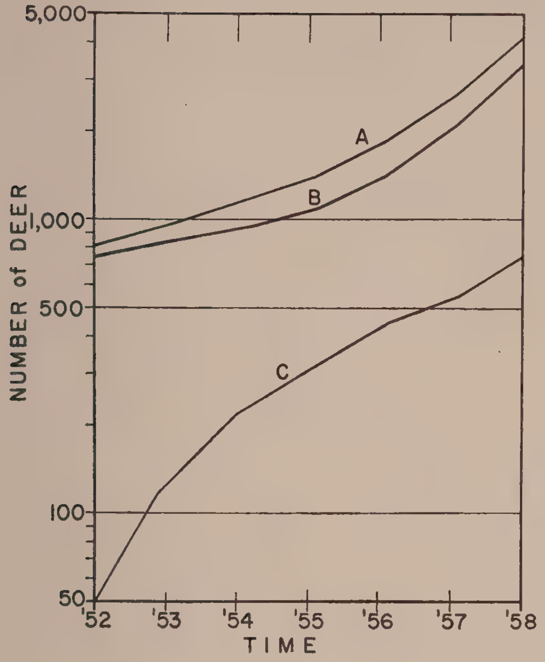

FIG. 3. Estimated unimpeded (A) and actual (B) rate of increase after hunting losses (C) of the Choccolocco deer population since 1952.

Distribution

Exclusive of the breeding season and especially manifest during the late summer after fawning, individual deer in the Choccolocco Area were probably distributed according to 2 broad patterns: mature males were randomly distributed, while the remainder of the population exhibited a randomly grouped distribution (Figure 4). Thus, exclusive of local habitat differences, sex and maturity were the dominant forces acting together to produce these 2 patterns of distribution within the population. Sexual maturity culminating in actual breeding was not accomplished by deer in the Choccolocco Area until they were at least 16 months old.

Within the aggregates, individuals remained together primarily as a result of social processes which tended to hold mother and fawn(s), mother and fawn(s) and yearling(s), or yearlings, together as family groups. Interfamilial groups may occur during the winter months since as many as 12 deer have been observed feeding and moving together as a unit or herd.

This spacing between groups and individuals has an as yet undetermined optimum which is governed by social intolerance and intraspecific competition inherent in deer populations. A breakdown in the spatial separation of these groups due to overcrowding and subsequent displacement of added groups into less favorable habitat may be a density dependent factor capable of producing or at least helping to produce widespread mortality.

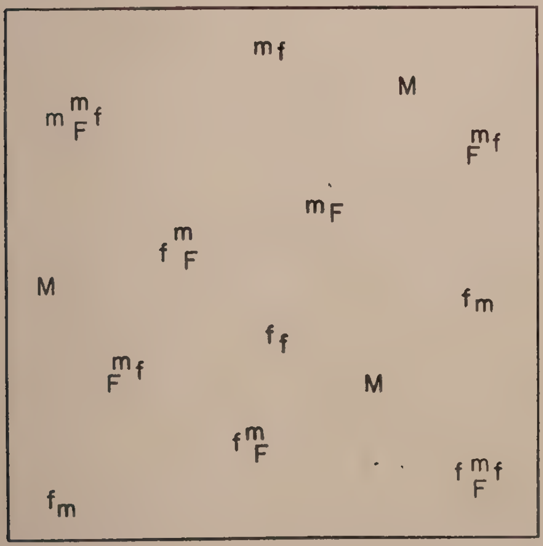

FIG. 4. Problematical late summer distribution patterns of deer in Choccolocco. Area of square represents 1 section or 640 acres.

M—mature male
m—immature male
F—mature female
f—immature female

TABLE V. Reproductive data of Choccolocco and captive does collected from 1957 through 1959

DOE AGE		PRIOR PREGNANCY		CURRENT PREGNANCY			APPROXIMATE DATE	
		Corpora		Corpora	Embryos			
Yr.	Mo.	Lutea	Fawns	Lutea	M	F	Conception	Birth
				Captive				
3	8			2	1	1	Jan. 18	Jul. 31
7	10	3	2	2	1	1	Jan. 8	Jul. 23
8	0	3	2	2		2	Jan. 27	Aug. 9
				Collected				
1	0[1]							
1	6			1	?		Dec. 1	Jun. 14
1	7			1	1		Dec. 4	Jun. 17
1	9			2	1		Dec. 24	Jul. 7
1	9			1		1	Dec. 11	Jun. 24
2	8			1		1	Dec. 10	Jun. 23
2	9[2]			2		2	Jan. 8	Jul. 22
2	10[2]		1	2	1	1	Jan. 10	Jul. 24
3	9	1	2	2		1	Dec. 15	Jun. 28
3	9	1		2		2	Dec. 14	Jun. 27
3	9[2]	2	2	2		1	Jan. 9	Jul. 23
3	10	2	1	2		2	Dec. 14	Jun. 27
4	7	2	2	2	2		Dec. 25	Jul. 8
4	8	2	2	2		2	Dec. 13	Jun. 26
5	7	1	2	2	1	1	Dec. 5	Jun. 18
5	8	2	2	2	1	1	Dec. 3	Jun. 16
5	9	1	2	2	1		Dec. 5	Jun. 18

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[1] Not pregnant.
[2] Probably conceived during second heat period.

Reproduction

Results of data from several sources were grouped together in order to determine the pattern of reproductive behavior in the Choccolocco Area (Table V). For purposes of computation, an average gestation period of 196 days derived from records of a Choccolocco doe maintained in pens at Auburn was utilized.

A regression analysis was run using 4 known age fawns obtained by Caesarean operations and a 17 mm embryo from a collected doe (Figure 5). Using this as a basis, all subsequent embryo lengths were plotted along this line in order to determine their approximate conception and birth dates. In the case of twins, a mean length was used.

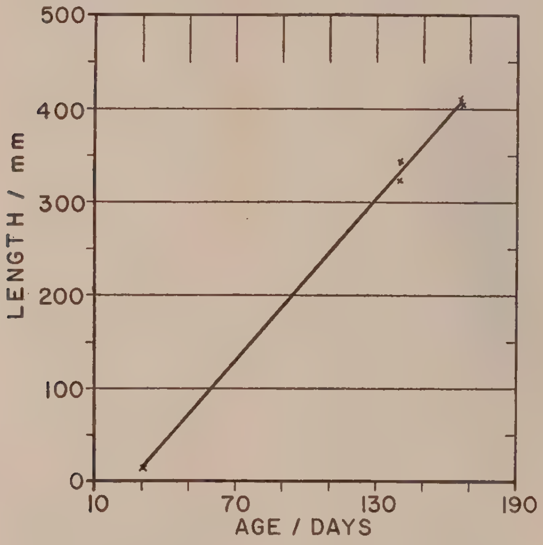

FIG. 5. Relationship of embryo length to known age. $Y = -68.3 + 2.87X$.

During the entire period of collection, every effort was made to determine the number of fawns surviving from previous pregnancies for each doe collected. In case of uncertainty, estimates were not recorded. This factor of known fawn survival correlated with their own corpora lutea scars and embryos of current pregnancies correlated with their corpora lutea provided a double element of certainty in estimating doubtful or incomplete pregnancy histories.

Breeding period.

Breeding among Choccolocco deer extended from late November through early January with a peak of activity during the first half of December. Atypical breeding between these dates may occur during any time of the year but is probably so rare that it contributes little if anything to changes in population density.

Pregnancy.

The known incidence of fertilization in relation to corpora lutea counts provided an index of reliability for predicting the incidence of fertilization in unknown cases. The utilization of embryo counts also aided in predicting the number of embryos per pregnancy in unknown cases. As a result of these determinations, it became apparent that does in the Choccolocco Area rarely if ever bred as fawns, they usually had single fawns during their first pregnancy and twin fawns during subsequent pregnancies. As previously mentioned, the first departure from this sequence was noted during the gestation period in 1959. Despite these aberrations, all reproductive tracts examined during this study showed evidence of successful fertilization after sexual maturity had been attained. Resorption of embryos was not evident in any of the specimens examined, although there was an obvious weight and length difference between sexes of twin pregnancies with the male larger in all cases. Twins of the same sex tended to be equal in length and weight. Of 23 sexable embryos collected, 8 were males and 15 were females.

Fawning period.

A peak in fawning occurred between mid-June and early July. The earliest fawn date was May 29 or 30 and the latest about mid-August. As an index of fawning success, separate cases of 21 does seem with single fawns, 16 does seen with twin fawns and one doe seen with triplets were recorded during the period of field investigations.

Statewide comparison.

Lueth (1955) stated that the fawning season in Alabama extended over a relatively long period of time with an average date of August 10. This figure was derived by using various data on a statewide basis. Since information from Choccolocco did not support these conclusions, it became necessary to determine why these discrepancies occurred. Reproductive data gathered in the field from Choccolocco were therefore compared with data gathered by Haugen (1959) using both Choccolocco and south Alabama deer (Table VI). Both field and experimental Choccolocco records displayed considerable similarity and together indicated a much earlier breeding cycle than that of south Alabama. These differences in reproductive patterns of deer from the 2 Alabama areas re-

TABLE VI. Differences in reproductive patterns of 2 populations of *Odocoileus virginianus*

POPULATION		CHOCCOLOCCO		SOUTH ALABAMA
SOURCE OF DATA		Field	Auburn pens	Auburn pens
BREEDING DATES	$\bar{x}$	Dec. 11	Dec. 31	Jan. 29
GESTATION PERIOD days	n		4	8
	$\bar{x}$	196[1]	196.2	192.5
	s		2.03	3.08
	$s_{\bar{x}}$		1.02	1.09
FAWNING DATES	$\bar{x}$	Jun. 24	Jul. 14	Aug. 10
BIRTH WEIGHTS pounds	n		7	11
	$\bar{x}$	[2]	6.5	5.6
	s		.543	.47
	$s_{\bar{x}}$		.205	.142

[1] Substituted.
[2] Unknown.

mained at significant levels despite their combined maintenance in Auburn over a period of years.

CONCLUSIONS

Deer in the Choccolocco Area have exceeded the carrying capacity of the range as a result of inadequate removal of surplus animals either by human activities or by natural mortality. Failure to remove these surplus deer has resulted in a high degree of utilization of food plants and a reduction in numbers and coverage of more palatable food plants. This condition of range deterioration was evidenced by the establishment of a browse line in areas of high concentration of deer, the increased number of spike antlers among young male deer and the reproductive disturbances exhibited by does during the 1959 gestation period.

The number of deer left after hunting may be referred to as the residual population. It is comprised of all age groups including the previous summer's fawn crop. Under optimum conditions, the residual population never exceeds the maximum number of deer that may be consistently and safely carried overwinter with minimal deer mortality and damage to the range.

Overpopulation

All factors considered, the Choccolocco range in 1958 would permit a residual population of 2,000 deer to be safely overwintered under normal conditions. Since the current annual rate of increase was approximately 530 young/1,000 deer in the original population, an annual surplus slightly in excess of 1,000 animals would have to be removed each year in order to prevent further range deterioration. This annual removal would not include the deer in excess of the residual population already on the Choccolocco range.

If adequate controls are not applied to this or any population in excess of the carrying capacity, not only will the range suffer but it is also likely that mass mortality will result. Similar conditions of a high deer population and inadequate removal were followed by a mass die-off among Choccolocco deer in 1949. Although the exact cause was never determined, reports indicated that an epizootic may have been the actual agent (Haugen 1949). Nicholson (1954) found that when animals invade a favorable habitat in which an expendable requisite has accumulated, they tend to multiply without check until virtually all of this requisite has been removed at which time the population necessarily crashes. The subsequent population increase is proportional to the accumulation rate of this requisite and produces a succession of oscillations which may be smaller than the initial one produced in the previously uninhabited environment. This process of explosive populations in new environments explains why mass die-offs might occur on the newly reoccupied Choccolocco range and not on the long-established and continuously occupied ranges of south Alabama.

A puzzling feature of the 1949 die-off was that it occurred when fewer deer were probably on the range than presently exist. Since 1954, intensified timber removal has apparently greatly increased the carrying capacity of the range over that existing in 1949 (Figure 6). This conclusion

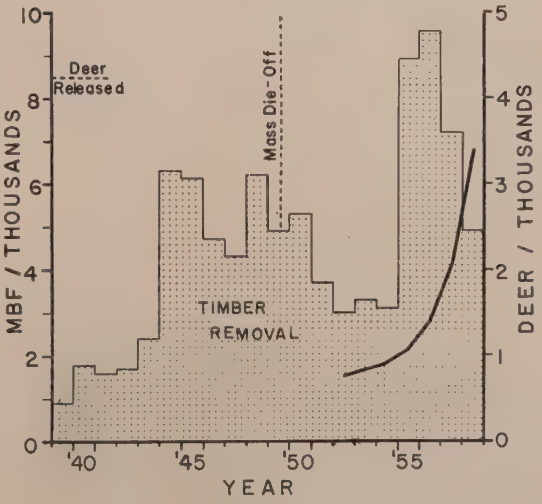

FIG. 6. Possible correlation between deer population increase and amelioration of the carrying capacity by logging operations in the Choccolocco Area.

has been borne out by previous investigations (Baskett, Dunkeson and Martin 1958).

Crowding is a contributing factor to mass mortality among deer but food may be equally important. Not only quality but also dispersion must be considered in interpreting food requirements. A deer has to move greater distances over greater periods of time at greater expense of energy as food becomes limited and more scattered than it would under optimum conditions of food abundance and concentration within its home range. This increasing dissipation of energy over a period of time produces physiological stress that further contributes to the mechanisms that reduce high densities of deer to lower levels. For this reason, degree of plant utilization alone may not be a true indication of range conditions unless correlated with dispersion and quality of food plants in relation to the home ranges or procurement fields of deer.

Despite the existence of these natural density-regulating mechanisms, reestablished and unmanaged populations of deer in the Southeast eventually reach a point of maximum expansion that tends to be explosive or eruptive unless checked by human interference (Figure 7). This condition exists because the environmental effect on the rate of reproduction requires longer to manifest itself than it does on physical condition, stamina and resistance to disease.

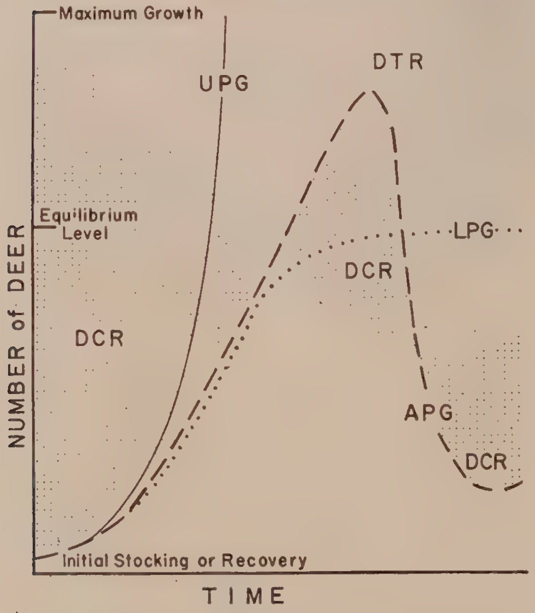

Fig. 7. Theoretical population increase and dynamics of deer populations in the Southeast, especially on newly established ranges. The 3 phases of population growth represented are unimpeded (UPG), limited (LPG) and actual (APG). Over a period of continuous occupancy, the actual growth curve undergoes a series of diminishing oscillations and tends to approximate the limited population growth curve. The density conditioned reaction (DCR) tends to reduce the rate of increase and functions at varying intensities during all stages of population growth. The density triggered reaction (DTR) produces mass mortality and functions for a brief interval during a peak in population growth.

SUMMARY

A study was made of the basic ecology and management of a white-tailed deer population in the Choccolocco Wildlife Management Area, Cleburne County, Alabama. Data for this study were gathered during 190 field days in the Choccolocco Area including managed hunts during 1956-57-58.

In addition to a study of population dynamics, a survey was made of the Choccolocco range. This survey was accomplished during the summer of 1957 and winter of 1958. One hundred line-intercepts 100 feet in length and 4½ feet in height were randomly distributed throughout the representative 16,000-acre Shoal Creek drainage. Vegetation in excess of 4½ feet was recorded as understory and canopy. Utilization of food items was determined from range survey and stomach samples.

Considerable data were obtained from records of all deer killed (legal and recovered illegal) in the Choccolocco Area since 1953. The relative age of deer was determined by using tooth development and wear as criteria. Pregnant does were collected at intervals throughout the 1957-58-59 gestation periods. The incidence of fertilization was determined by an examination of ovaries for corpora lutea. Age of embryos was determined by comparing them with known-age embryos obtained from captive deer.

Hardwoods in the Choccolocco Area progressively declined in importance from stream bottoms to ridge crests. Site-moisture relationships had a pronounced effect on the distribution of forest types. The range survey indicated that low-bush blueberry was the most important browse species on an annual basis. Other heavily utilized plants included greenbrier, hydrangea, dwarf sumac, strawberry-bush, mountain laurel, sweetleaf, viburnum and black gum. In addition to supporting range survey findings, stomach samples revealed the importance of acorns, fungi, lichens and litter in the diet of deer.

Range deterioration was evidenced by over-browsing of many important food plants and the establishment of a browse line in areas of high

deer concentrations. This condition was correlated with increased numbers of younger bucks with spike antlers and does in poor physical condition with single embryos after initial pregnancy. The coaction of weather and other environmental factors was reflected in reduced hunting success following a summer drouth and a severe winter.

Where natural predators have been exterminated from deer populations, man has assumed the role of predator and tended to reverse the natural selectivity of age and sex among the prey. The Choccolocco deer population in early 1959 consisted of approximately 2,000 breeding animals with a sex ratio of 1 male to 3 females and a previous summer crop of 1,500 fawns. These deer tended to be distributed throughout the Choccolocco Area as random individuals and family aggregates as a result of the interaction of sex and maturity. Peak breeding occurred during the first half of December with subsequent fawning between mid-June and early July. Does rarely if ever bred as fawns, they usually had single fawns during their first pregnancy and twin fawns during subsequent pregnancies.

The present Choccolocco deer population has exceeded the optimum carrying capacity because of inadequate removal of surplus animals. A combination of factors similar to those now in operation on the Choccolocco Area culminated in a die-off of mass proportions in 1949. Indications are that when the rate of reproduction exceeds the rate of range deterioration, mass die-offs of deer populations in the Southeast may occur before fecundity is reduced.

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[1] A contribution of the Alabama Cooperative Wildlife Research Unit, the Auburn University, the Alabama Department of Conservation, the Wildlife Management Institute and the U. S. Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, cooperating. This paper was awarded an Honorarium by the American Society of Mammalogists in 1959.

A SURVEY OF THE HETEROTROPHIC BACTERIA IN SANCTUARY LAKE OF THE PYMATUNING RESERVOIR[1]

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INTRODUCTION

A study of the heterotrophic bacteria in Sanctuary Lake of the Pymatuning Reservoir offered a unique opportunity to investigate the effect of pollution on a controlled water area used as a wildlife sanctuary. Many other facets of the ecology of this lake had been explored by previous researchers. Studies had been made of its fish (Marcy 1953), birds (Davis 1943), and plankton (Tryon and Jackson 1952, Borecky 1956) but this was the first bacteriological study to be made in these waters.

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[1] Publication No. 22 of the Pymatuning Laboratory of Field Biology of the University of Pittsburgh.

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Pymatuning Reservoir, located in northwestern Pennsylvania and northeastern Ohio, is 17 miles long, has 70 miles of shore line, and covers approximately 17,000 acres. The reservoir was filled in 1934 by the completion of a pair of dams across biologically rich Pymatuning Swamp, one at the northern end near Linesville, and one at the southern tip near Jamestown. A causeway was constructed across the reservoir near Epsyville. The reservoir may be divided into three major areas: Sanctuary Lake, Middle Lake and Lower Lake (Fig. 1).

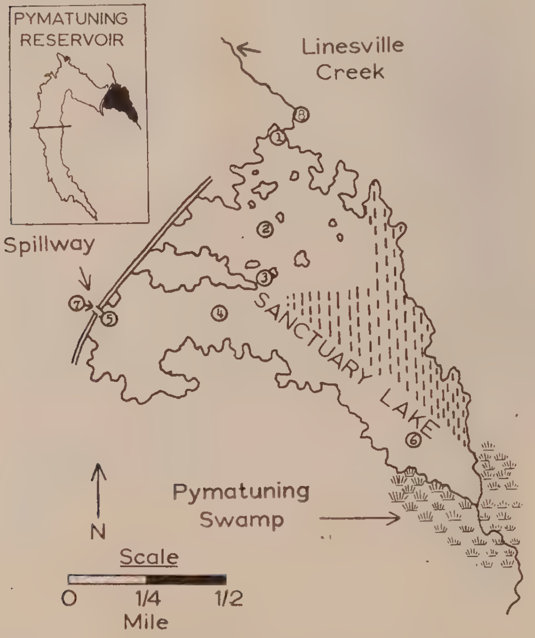

Fig. 1. Outline map of Sanctuary Lake showing the locations of sampling stations. Shaded area of the inset map shows position of Sanctuary Lake in Pymatuning Reservoir.

Sanctuary Lake is separated from Middle Lake by the Linesville Causeway and flows into Middle Lake by means of a spillway. Sanctuary Lake, a very shallow, eutrophic body of water with a mean depth of about 5 ft, is a wildlife preserve. It supports an abundance of aquatic life. The water is alkaline and contains a relatively large amount of organic matter in solution. Tryon and Jackson (1952) found this lake had a high plankton productivity and a greater amount of suspended organic matter than any body of water previously described. This large quantity of available organic matter makes Sanctuary Lake ideal for bacteria.

Although Middle Lake and Lower Lake are separated by the Epsyville Causeway, they are connected through two openings in the causeway. The mean depth of Middle Lake is approximately 12 ft and that of Lower Lake is 18 ft. Together they cover approximately 14,500 acres. At the southern end of Lower Lake is a dam, regulated by the Pennsylvania Department of Forests and Waters, which impounds the water. Fishing and recreational use are provided in both Middle and Lower Lakes.

The Pymatuning Reservoir is intended to serve three primary purposes: to maintain a minimum low-water flow in the Shenango and Beaver Rivers, thereby improving sanitation and providing an adequate water supply for domestic and industrial use; to reduce flood flow; and to create a good recreational area and wildlife sanctuary. These values must be balanced against the artificial modification of the previous outstanding natural area.

The approximately 2,500 acres of Sanctuary Lake lie within a wildlife preserve of the Pennsylvania Game Commission, where the Pennsylvania Fish Commission maintains its largest fish hatchery. The Pymatuning Laboratory of Field Biology of the University of Pittsburgh is also located within the preserve, but aside from these facilities Sanctuary Lake is restricted from public use.

Sanctuary Lake has two main sources of inflow. The larger of these is from Linesville Creek, which enters the northeastern end of the lake. The smaller inflow is from Pymatuning Swamp. Linesville Creek contains raw sewage from Linesville, a town with a population of 1,100. It also drains an agricultural area and contains wastes from a diary. Pymatuning Swamp drainage takes care of inflow from the remainder of the original swamp.

Since the primary concern of this study was the effects of the pollution from Linesville Creek on the bacterial population of Sanctuary Lake, a series of 5 sampling stations was set up in a line extending from the mouth of Linesville Creek to the spillway where Sanctuary Lake empties into Middle Lake. A 6th station was located near the mouth of Pymatuning Swamp. Stations 1, 2, 3, 4 and 5 could receive drainage from Linesville Creek. Stations 4, 5 and 6 could receive drainage from Pymatuning Swamp. These two drainages are somewhat separated in the lake by a large area of emergent vegetation except at the western end of the lake. Later, Stations 7 and 8 were added. Station 7 was located in the spillway connection between Sanctuary and Middle Lakes. Station 8 was in Linesville Creek about ¼ mile upstream from its mouth.

MATERIALS AND METHODS

A Kemmerer water sampler (Foerst modification) was available at Pymatuning but was not used because the large number of samples needed would have created a sterilization problem. Many other types of water samplers were considered but were rejected as too complicated. It was therefore decided that a sampler should be designed and built to meet the specific needs of this problem. The resulting equipment, described completely by Morgan and Gainor (1960), is simple in construction, effective, and easily sterilized. It will obtain one-pint samples at a given depth and is especially useful in shallow lakes and small streams or rivers.

Water samples were collected from a boat at each of the first 6 stations about twice a week from June 24 to August 27, 1950. Two samples were collected at each station. The first, designated sample A, was collected a few inches below the surface; the second, designated sample B, was obtained at a depth of 36 in.

Water samples were stored in an ice chest between the time of collection and return to the laboratory for experimental analysis, the time lag being about 1½ hr between collection and cultivation. All preliminary isolations and tests were conducted at the Pymatuning Laboratory of Field Biology during the summer period. Other studies were carried out at the University of Pittsburgh.

When ice thickness permitted, samples were collected periodically at the first 6 stations between September 1950 and June 1951. During this time samples were also collected a few inches below the surface at stations 7 and 8.

After collection at Pymatuning, these samples were iced, if necessary, inoculated into appropriate media, and brought to the University of Pittsburgh by automobile, incubated enroute by an automobile heater. The incubation and other tests were completed in Pittsburgh.

A conventional bacteriological incubator was not available at Pymatuning, so a cylindrical egg incubator was modified for usage. A piece of sheet metal was used to increase the inside height to 18 in. to accommodate test tube racks, and three 50-watt electric light bulbs covered with aluminum foil were used to augment the heating unit. A pie plate filled with water was placed in the bottom of the incubator to prevent evaporation and desiccation of the media. With these modifications the thermostat maintained a temperature of 37°C ± 2°. All material cultured at the field station was incubated under these conditions for 24 to 48 hr.

All media, water dilution bottles, and sample bottles were sterilized in a small electric autoclave. A gas kitchen oven was used to sterilize petri dishes and pipettes.

A quantitative estimate of the coliform bacteria was obtained by the Coliform Indicated Number Test (Standard Methods 1946) as follows. Aliquots of the sample containing 5.0, 1.0, and 1/10 ml, as well as one ml quantities of a 1/100, 1/1000, and 1/100,000 dilutions were inoculated into lactose broth. Eosin methylene blue agar plates were streaked from the positive lactose presumptive tubes for confirmation.

The procedures for these two tests, as well as for the Completed Test, are noted in Standard Methods (1955). The above tests were performed at Pymatuning, while the partial identification of the organisms was undertaken at the University of Pittsburgh.

The 15 tube Most Probable Numbers Test would have been better to use than the Coliform Indicated Numbers Test (CIN). However, because of lack of incubator space this was impossible.

Standard plate counts were made with aliquots of 1.0 ml, as well as one ml quantities of 1/100, 1/1000, 1/10,000, and 1/100,000 dilutions, using Tryptone Glucose Extract Agar (TGEA). Typical and atypical coliform organisms were isolated for identification.

Enteric bacteria cultured from tethrathionate broth were subsequently isolated from SS agar plates and identified.

Thioglycollate medium and cooked meat phytone medium were used to cultivate anaerobic bacteria. With the exception of the cooked meat phytone medium from the Baltimore Biological Laboratory all bacteriological products were Difco.

To ascertain effects of weather on bacterial numbers, records were kept throughout the study. These were further checked against United States Weather Bureau data taken at the southern tip of Pymatuning Reservoir at Jamestown. Conditions recorded were rainfall, average temperature, prevailing wind, and sky cover.

RESULTS AND DISCUSSION

During the study, 312 samples were collected to obtain Coliform Indicated Numbers at both depths at the 6 stations within Sanctuary Lake. These data furnished information on the horizontal and vertical distribution of coliform organisms within the lake. Similar readings were taken at Stations 7 and 8, control points situated outside Sanctuary Lake. Because the water was so shallow at these latter stations, they provided only horizontal distribution data.

The CIN for Stations 1, 6, 7, and 8 on various sampling dates are presented in Table I. Stations 2, 3, 4 and 5 did not furnish significantly high CIN readings except on August 19, 1950, after a severe wind and rain storm. At that time readings at Stations 2A and 2B were each 10/ml; and on March 7, 1951, the reading at Station 5A was also 10/ml. On all other sampling dates the readings at both depths for these 4 stations ranged between 0/ml and 4/ml, but were most frequently either 0/ml or 1/ml.

TABLE I. Coliform Indicated Numbers of stations 1A, 1B, 6A, 6B from 6/24/50 to 6/17/51, and of stations 7 and 8 from 9/30/50 to 6/17/51. The low values obtained at stations 2A through 5B are described in the text

Date	Stations					
	1A	1B	6A	6B	7	8
6/24/50	310	500	1	1		
6/27/50	260,000	260,000	1	2		
7/5/50	180,000	180,000	2	5		
7/8/50	180,000	180,000	0	0		
7/11/50	44,000	61,000	1	3		
7/15/50	170,000	180,000	1	4		
7/18/50	240,000	240,000	1	3		
7/22/50	170,000	180,000	2	6		
7/25/50	230,000	230,000	1	3		
8/1/50	170,000	180,000	2	4		
8/5/50	170,000	180,000	0	0		
8/8/50	690	410	1	3		
8/12/50	220,000	240,000	0	0		
8/15/50	90,000	91,000	0	0		
8/19/50	1,000,000	1,000,000	10	10		
8/22/50	1,600	600	1	1		
8/27/50	1	0	1	2		
8/29/50	80,000	80,000	0	0		
9/30/50	19,000	4,200	0	0	1	1,000,000
10/29/50	180,000	190,000	33	1	3	2,400,000
12/30/50	1,300	3,300	2	0	0	810,000
3/7/51	810,000	850,000	100	10	11	5,700,000
5/12/51	20,000	31,000	65	3	6	1,100,000
6/17/51	210	520	3	0	0	790,000

Station 1 shows no difference in the vertical distribution of coliform organisms. The lake depth at the mouth of the creek is only 3 ft, and the turbulence gives a homogeneous distribution. For other stations at all seasons of the year, with the exception of summer, the highest number of coliforms occurred at the surface level.

The horizontal distribution of coliform bacteria proceeded in a decreasing order from the point where sewage enters Linesville Creek at Station 8 to the point where Sanctuary Lake empties into Middle Lake at Station 5. The numbers of coliform at Stations 8 and 1 were very high, with a sharp reduction as Linesville Creek enters the lake. On September 30, 1950, for example, the CIN at Station 8 was 1,000,000 per ml; at Station 1A, it was 19,300 per ml; at Station 1B, it was 4,200 per ml; at Stations 2A, 2B, 3A, 3B, 4A, 4B, and 5B the reading was 0.

Several factors could contribute to this decrease. The first is the self-purification of a flowing stream, although this is somewhat offset by the fact that the distance from the entrance of sewage into the lake at Station 1 to the second sampling point at Station 2 is approximately ¼ mile.

A second factor is the relative volume of the creek as compared to that of the lake. Some decrease in bacterial numbers could be attributed to dilution.

A third factor is predatory organisms. Bacteria are known to be utilized as food by protozoa (Henrici 1948). Orr (1954) found that raw sewage from Linesville Creek may result in an increase in bacterial numbers and thus favor holozoic types of protozoa. A large concentration of protozoa at the mouth of a polluted river where it entered Lake Ontario was also found by Whipple (1927).

A fourth factor is sedimentation. Henrici (1948) found that a reduction in the number of bacteria entering a lake from a stream was due to absorbtion of bacteria onto larger particles suspended in the water and subsequent settling out of these particles.

Prevailing winds were the fifth factor. Whipple (1927), in his study of the Genesee River, found that the perimeter of pollution was extended farther into Lake Ontario with offshore than with onshore winds. At Pymatuning Reservoir it was found that offshore or northerly winds gave higher counts of coliform organisms at Station 1 with a linear correlation coefficient. Southerly or onshore winds gave lower counts of coliform organisms.

Four hundred and twenty-two cultures were subjected to the Completed Test. At all except Station 6, the majority of the coliform organisms found were *Escherichia coli,* with a small number of *Aerobacter aerogenes* and other coliform intermediate types present. At Station 6 the predominant coliform was *A. aerogenes,* with other types found occasionally. No accurate counts were made of the relative numbers of each type of coliform colony on the confirmatory medium.

The following coliform organisms were identified according to the criteria given in Bergey's Manual (Breed *et al.* 1948), after having been

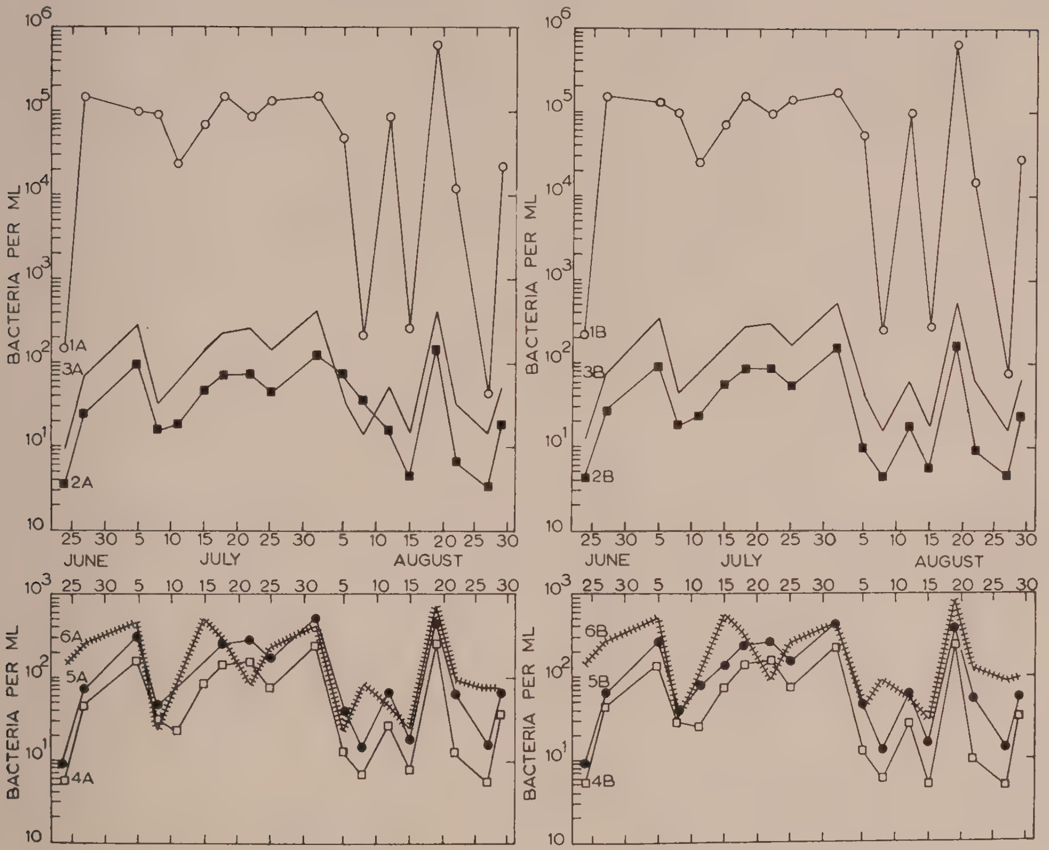

FIG. 2. Graphs of stations 1A through 6B showing the Standard Plate Count of bacteria during the 70 day summer period.

subjected to the Completed Test as in Standard Methods page 377, section C (1955), and found to give positive reactions: *E. coli, E. freudii, E. intermedia, A. aerogenes,* and *A. cloacae.*

Results of the 312 Standard Plate Counts are presented in Figure 2. These cover an intensive 70 day sampling period during the summer of 1950. Not included in Figure 2 are results of the subsequent 3 seasons which were found to be typical of the data already plotted. The entire data are available (Morgan 1958). According to the horizontal distribution the largest numbers of bacteria were found at the stations nearest the two sources of drainage. This is comparable to the type of horizontal distribution found in Lake Mendota by Fred, Wilson, and Davenport (1924).

The patterns in the horiontal distribution of bacteria at the various stations, as demonstrated by the Standard Plate Count, were erratic. The highest counts of bacteria in the lake itself were at Stations 1 and 6, both of which were at the mouth of a drainage area. The next highest number of bacteria was at Station 5, where organisms could have been received from both these drainages. Station 3 was littoral in nature, which could explain its relatively high counts. The counts of bacteria were greater at Station 4 than at Station 2, as Station 4 could receive drainage from both inflows, while Station 2 receives drainage from only one inflowing stream.

The vertical distribution of bacteria, as measured by the Standard Plate Count, indicated greater numbers at the 3 ft depth than at the surface for all stations except Station 5. This demonstrates the sedimentary effect of bacteria being absorbed onto larger particles and settling out. At Station 5 such particles could have settled below the 3 ft level, as this station is in the deepest area of the lake.

Bacteria which were isolated from the TGEA plates and subjected to the criteria as noted in Bergey's Manual (Breed *et al.* 1948) yielded the following predominating genera and species: *Achromobacter delicatulus, Alcaligenes faecalis,* *Alcaligenes recti, Bacillus subtilis, Bacillus megatherium, Flavobacterium invisible, Flavobacterium breve, Paracolobacterum aerogenoides, Proteus vulgaris, Pseudomonas aeruginosa, Pseudomonas ambigua, Pseudomonas rugosa, Sarcina flava, Serratia marcescens* and *Streptococcus lactis.* Since a number of deletions and alterations have appeared in the latest edition of Bergey's Manual (Breed *et al.* 1957), and since a number of closely related species differ in but one or two characteristics, the authors have chosen to limit the listing of organisms as above.

Salmonella enteritidis and *Shigella sonnei* were isolated from selective media and identified according to morphological and biochemical characterizations in Bergey's Manual (Breed *et al.* 1948). Similarly identified were *Clostridum perfringens* and *Streptococcus faecalis,* which were isolated anaerobically.

Weather data recorded during the study are reported in Table II. In analyzing this information, however, only 70 days during late June, July, and August of 1950 were considered. This was done so that sufficient water samples could be compared with the weather data.

TABLE II. Weather data at Sanctuary Lake. Sky cover designation is described in the text. Rainfall is total rainfall from the previous sampling date except from 9/30/50 to 6/17/51, when only rainfall during the 4 days previous to sampling is included

Date	Prevailing Wind	Average (Temp. (F)	Sky Cover (Sunrise-Sunset)	Rainfall (In. Bet. Samp)
6/24/50......	SW	77	8	0.00
6/27/50......	WNW	62	6	0.38
7/5/50.......	SW	67	8	0.95
7/8/50.......	NE	67	2	0.00
7/11/50......	SW	68	9	0.12
7/15/50......	SSW	67	4	0.57
7/18/50......	WNW	66	5	0.79
7/22/50......	SSE	67	4	0.79
7/25/50......	W	69	6	0.48
8/1/50.......	WSW	79	8	0.78
8/5/50.......	NW	65	4	1.02
8/8/50.......	S	69	4	0.00
8/12/50......	NNE	62	4	0.02
8/15/50......	ESE	69	4	0.00
8/19/50......	NE	65	9	0.49
8/22/50......	SW	61	0	0.00
8/27/50	SSW	75	5	0.00
8/29/50......	WSW	73	8	0.03
9/30/50......	SE	57	4	0.00
10/29/50.....	SW	63	7	Total 0.62
12/30/50.....	S	27	10	of 0.03
3/7/51.......	W	51	8	Four 2.51
5/12/51......	WNW	54	4	Previous 1.06
6/17/51......	SE	70	4	Days 0.00

A numerical value is given for sky cover. This was obtained by establishing the values 0-3 for a clear day, 4-7 for a partially cloudy day, and 8-10 for a cloudy day.

During the 70 days of intensive study in the summer of 1950, there was no apparent correlation between air temperature or sky cover and the bacterial populations measured. Both rainfall and wind direction, however, exerted influence on bacterial numbers.

During the 70 day period the rainfall of the area was approximately normal except for the month of August, when it was about 2 in. below normal. To investigate the effect of rainfall on the bacterial populations, the total rainfall between two bacterial samplings was used and applied to the second sampling. This information appears in Table II.

When the total amounts of rainfall between samplings were compared with CIN data, no significant correlation was found at the 95% confidence level. The data indicated, however, that a curvilinear correlation does exist. Similar data have been recorded for some English lakes (Taylor 1941).

The effects of rainfall were more apparent with the Standard Plate Counts than with CIN data. The Standard Plate Counts can be increased by runoff from any portion of the shoreline, while the coliform organisms originate at Stations 1 or 6 and must be transported to the other stations.

When rainfall data were compared to Standard Plate Count samples there were linear correlation coefficients which in some cases were at the 95% confidence level. All stations indicated some correlation, with some showing a curvilinear function.

Prevailing wind data can be converted to a numerical value by recording the wind direction as the number of degrees it deviates from true north. When these values were applied to the CIN readings, linear correlations were usually found with significant relationship at the 95% confidence level. The linear correlation between coliform organisms and wind direction indicated a reduction in bacterial numbers as the prevailing winds came from a more southerly direction. This was especially apparent at Station 1A.

Prevailing winds were more significantly correlated with CIN counts than with the number of organisms measured by Standard Plate Counts. There was no correlation at the 95% confidence level between prevailing wind and Standard Plate Counts, but correlation at a lower level did exist at times. Curvilinear relationships were found between wind direction and Standard Plate Counts. The Standard Plate Counts were lowered as the prevailing winds came from a more southerly direction.

Rainfall and prevailing wind directions were able to offset or intensify each other in their effects on the bacterial populations.

This preliminary investigation was intended to stimulate future bacterial research in this lake. If more is to be learned of the ecology of these and other bacterial populations, a more intensive year-round study must be made. The intensive summer study indicates some of the factors which play a part in the control of bacterial populations.

SUMMARY

Sanctuary Lake is a shallow eutrophic lake which receives water from two drainages. Linesville Creek contains raw sewage and agricultural drainage. Pymatuning Swamp also contains drainage from agricultural lands. The water from these two drainages is separated in the lake by an area of emergent vegetation except at the western end of the lake. Sanctuary Lake supports an abundance of aquatic life.

The high concentration of coliform organisms in Linesville Creek was greatly reduced as its waters entered Sanctuary Lake. The reduction continued as these organisms were horizontally distributed across the lake until they almost or entirely disappeared. The vertical distribution of these coliform organisms indicated that sedimentation occurs.

The Linesville Creek drainage contains large number of *E. coli,* while the Pymatuning Swamp drainage contains large numbers of *A. aerogenes.*

The number of organisms measured by the Standard Plate Count was reduced upon entering the lake from the drainage areas. However, significant amounts of these organisms were distributed horizontally across the lake. Other run-off could increase these counts. These organisms also were sedimented, as evidenced by their vertical distribution.

Average temperature and the amount of sunshine had no apparent effect on the distribution of the bacterial populations.

Rainfall and prevailing wind direction had an apparent effect on the bacterial populations but were able to offset or intensify each other in their effects.

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THE COMPOSITION OF SAVANNA VEGETATION IN WISCONSIN

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Savanna is defined, following Seifriz (1943), as any grassland in which there are open-grown trees of scattered distribution. A degraded forest is thus not a savanna, nor is the ecotone between taiga and tundra, since the ground cover is not primarily grassy. The major vegetation types in Wisconsin delimited by this definition are the Quercus openings, or as sometimes designated, Quercus islands or Quercus groves, the Juniperus glades, Ulmus groves, and Ulmus-Fraxinus groves. The present study summarizes field work during the summers from 1951 to 1955 and includes a description of the composition of savanna communities in Wisconsin and observations on some environmental relations of these communities.

Drs. J. T. Curtis, Grant Cottam, and A. G. Vestal provided valuable criticism and discussion during this study. Mrs. M. S. Bergseng, Dr. H. C. Greene and Dr. James Zimmerman aided in identification of plants. Special thanks are due Drs. Orlin Anderson, R. T. Brown, R. T. Ward, G. H. Ware, Miss Lorry Miller, and Mr. H. G. Liebherr for aid in collection of field data.

This study was supported in part by a grant from the Graduate School of the University of Wisconsin from funds supplied by the Wisconsin Alumni Research Foundation.

Nomenclature is after Gleason (1952). *Quercus ellipsoidalis-velutina* represents a population which could not be separated into distinct taxa.

Description of the Region

Savanna in Wisconsin occurs within the overlapping region of prairie distribution presented in Curtis (1955) and of forest distribution mapped in Curtis and McIntosh (1951). The location of sampled savanna stands is shown in Fig. 1.

A general description of the physical features of the region in Fig. 1 is given in Curtis (1959). Climatic factors include cyclic mild to severe summer droughts, a snowfall less than 45 in., a mean summer temperature of 68°F, 60 or more days in which the temperature is above 68°F, and a July evaporation of 5 or more in. There is no apparent correlation of savanna with geologic or physiographic province or with soil type.

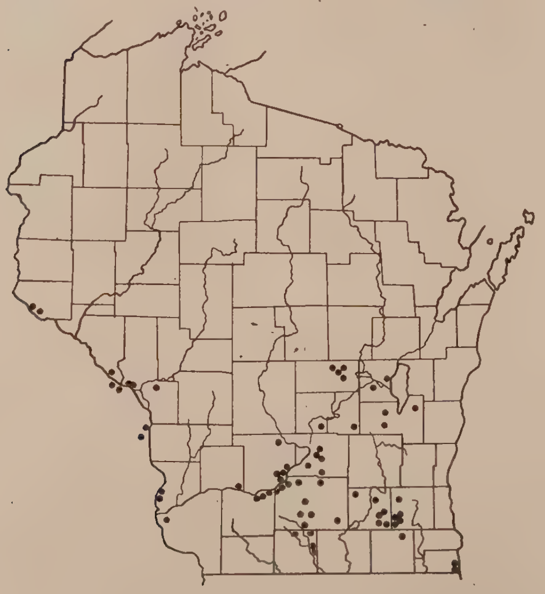

Fig. 1. Geographic location of sampled stands.

Location and Selection of Stands

In searching for undisturbed savanna vegetation, no tree stand in which there was cutting and no understory which had not recovered from grazing was investigated. A grazed stand was recognized by the decreased importance of native forbs and grasses and by the presence of weedy native plants and of exotics. Many stands were rejected in which past grazing had removed most of the prairie grasses, but in which many prairie forbs had survived and were rapidly regaining their former importance. The criterion for separating savanna from forest was necessarily arbitrary, with savanna considered to be any stand in which canopy openings prohibited all or a substantial part of an individual tree canopy from contact with its nearest neighbors. The selected stands varied from a few trees per acre to fairly dense woods in which an occasional opening persisted and in which the canopy approached 60% cover. Areas in which undisturbed savanna was found included: (1) low meadows and prairies in eastern Wisconsin in which there was inadequate drainage for crops and in which there had never, or rarely, been grazing; 2) thin soil, gravelly slopes of the Kettle Moraine in eastern Wisconsin which were lightly grazed for some time prior to the drought of the 1930's and are at present protected by state ownership; 3) sand areas in southern and central Wisconsin which have never been used agriculturally and are still subject to burning; and 4) hillsides and bluffs along the Wisconsin and Mississippi Rivers which are too steep to be cropped or grazed by cattle. Several areas were found which had been included in a non-farming estate. Savanna on slopes and bluffs in western Wisconsin was especially valuable since it often represented sites with a mesic understory flora which filled in gaps left by the agricultural use of all the drained flatland and rolling land savanna.

Sampling Methods

The random pairs technique (Cottam and Curtis 1949) was used to sample trees. Because of the scarcity of savanna stands, areas as small as 3 acres were included. In small stands which contained one or 2 species, a minimum of 20 points were sampled; in larger stands, 40 points were sampled. A total of 60 tree stands were surveyed.

Each of these stands contained an undisturbed arboreal layer but in 18 stands there was a grazed understory. Presence of tree seedlings, shrubs, and herbs was recorded from 1 x 1 m quadrats within the 42 stands with undisturbed understory. These quadrats were laid randomly within the stand, usually at each tree point, or along contiguous transects.

Eighty-two understory stands were surveyed in 49 separate geographic locations. Forty-two of these locations were in the tree stands, as noted. The remaining 7 locations were in prairie areas which contained only a few scattered trees or which were too small (i.e. less than 3 acres) for a tree survey. Within these 7 remaining locations, transects studies, as subsequently discussed, were conducted. These studies contributed 40 sets of homogeneous data which were each considered as separate understory stands. Within the 82 understory stands, 1,760 1 x 1 quadrats were examined for species presence.

Soil samples of the A_1 horizon from 3 soil profiles in each stand were analyzed compositely for certain chemical properties by the State Soils Laboratory, Madison, Wisconsin. Light intensity was measured within stands and over individual quadrats. The methods and some results of this study have been presented in Bray (1958).

Techniques used to record and compile vegetation data follow Curtis and McIntosh (1951). One tree stand was discarded in the laboratory, because of lack of homogeneity caused by an attempt to separate in the field an intergrading population of *Quercus velutina* and *Quercus borealis* which lay along a topographic gradient. As a result 2 blocks contained *Quercus velutina* and 2 had *Quercus borealis* and the stand was heterogeneous.

RESULTS AND DISCUSSION

In presenting results, a separate analysis of tree and understory data is necessary since 18 of the tree stands were grazed and were not investigated for understory composition.

Tree Stand Composition

Forty species of trees were found in the 59 homogeneous stands surveyed; 31 of these occurred as adults. Of these, 6 species, *Juniperus virginiana* (5), *Quercus ellipsoidalis-velutina* (19), *Q. alba* (7), *Q. macrocarpa* (13), *Q. bicolor* (4) and *Ulmus americana* (5) accounted for 90% of the sum of all importance values (Brown and Curtis 1952). Numbers in parentheses indicate stands in which the species was "dominant"; that is, in which it had the highest importance value. Other dominant species were *Carya ovata*, *Tilia* "xeric" (*americana-neglecta* complex) *Betula nigra,* and *Acer saccharinum* in one stand each, and *Quercus borealis* in 2 stands.

A matrix was constructed for the 6 most important species which contained the mean importance value (I.V.) of each species for each set of stands in which a given member of the 6 species occurred with an I.V. of 50 or higher. This matrix represents a modification of the leading dominant table (No. II) in Curtis and McIntosh (1951). The matrix was ordered by trial and error placement and a linear arrangement resulted with *Juniperus virginiana* and *Quercus bicolor* as the 2 endpoints, and with the other 4 species in intermediate order as listed above. A set of adaptation numbers was assigned to the 6 dominant species based on this order and a preliminary ordination of the 59 stands was constructed, using the technique of Brown and Curtis (1952).

The alignment of species along this preliminary gradient suggested minor modifications in 2 adaptation values which would bring them into greater symmetry with the locus of the species along the gradient. In addition, adaptation values, based on preliminary gradient location, were assigned to 9 other species, including all those which reached dominance. These assigned values are listed in column 1 of Table 1 and vary from 1.0 for *Juniperus virginiana* and *Tilia americana-neglecta* complex to 5.0 for *Acer saccharinum* and *Betula nigra.*

The final ordination was constructed by weighting the I.V. of each species by the adaptation value of the species and dividing the sum of these weightings by the sum of the I.V's. The theoretical range of ordination location was, therefore, from 1.0 to 5.0 and this range was divided into 5 sections of equal magnitude. The mean I.V. for each of the 31 adult tree species was then calculated for each of these 5 sections. Results are in columns 2 through 6 of Table I.

The usefulness of the assigned adaptation values is demonstrated by the ordered species amplitudes in Table I. Had a random set of adaptation values been assigned there would be no appreciable difference in species composition in the various intervals of the ordination. However, these distributions do not represent an idealized or average composition for a stand in any given gradient interval. For example, *Quercus macrocarpa* and *Q. alba* have a moderate overlap of amplitude in Table I and yet, for possible historic reasons, they do not usually occur together with a high I.V. in the same stand. However, if 2 species, such as

Table I. Ordination of tree species by mean importance value per ordination interval. A.V. is assigned adaptation value

	A. v.	ORDINATION INTERVAL				
No. of Stands		1 5	2 27	3 14	4 6	5 7
Juniperus virginiana	1.0	72.4	2.6	0.0	0.0	0.0
Populus grandidentata	1.5	4.4	0.5	0.0	0.0	0.0
Ostrya americana	—	1.6	0.0	0.1	0.0	0.0
Tilia americana-neglecta complex	1.0	2.4	1.0	0.0	0.0	0.0
Pinus banksiana	—	0.0	0.1	0.0	0.0	0.0
Betula papyrifera	1.5	2.2	1.2	2.4	0.0	0.0
Quercus ellipsoidalis-velutina	2.0	9.3	55.2	10.4	4.5	0.2
Quercus alba	2.5	2.1	20.1	1.3	0.7	0.5
Populus tremuloides	—	0.4	0.8	0.7	0.0	0.0
Prunus serotina	—	0.0	1.3	1.0	0.0	0.0
Carya ovata	2.5	1.8	4.1	7.5	5.1	0.0
Acer negundo	—	0.0	0.0	0.2	0.0	0.0
Juglans nigra	—	0.0	0.0	1.6	0.0	0.0
Quercus macrocarpa	3.0	0.4	10.4	65.9	14.4	1.2
Quercus borealis	3.5	2.4	1.8	2.7	7.8	0.5
X Quercus bebbiana	—	0.0	0.1	0.3	0.9	0.0
Crataegus sp.	—	0.0	0.0	0.0	0.3	0.0
Ulmus rubra	—	0.0	0.1	2.1	0.0	3.3
X Quercus schuettii	—	0.0	0.0	0.0	2.5	0.5
Fraxinus americana	—	0.0	0.0	0.5	0.0	0.8
Tilia americana	3.5	0.0	0.0	0.9	3.4	4.0
Fraxinus pennsylvanica	4.5	0.0	0.0	0.8	10.0	8.8
Ulmus americana	4.5	0.0	0.2	1.0	30.9	27.6
Quercus bicolor	4.0	0.0	0.0	0.0	16.5	24.3
Carya cordiformis	—	0.0	0.0	0.0	0.4	1.9
Acer saccharinum	5.0	0.0	0.0	0.0	1.6	15.0
Betula nigra	5.0	0.0	0.0	0.0	0.5	6.8
Acer saccharum	—	0.0	0.0	0.0	0.0	0.3
Fraxinus nigra	—	0.0	0.0	0.0	0.0	2.9
Larix laricina	—	0.0	0.0	0.0	0.0	0.2
Populus deltoides	—	0.0	0.0	0.0	0.0	0.2

Juniperus virginiana and *Quercus bicolor,* do not overlap along the gradient, they cannot be found together in the same stand.

The pattern in composition in Table I is initiated from the left by Juniperus glades strongly dominated by *Juniperus virginiana* and with various combinations of minor species including *Betula papyrifera, Tilia* "xeric," *Populus grandidentata, Ostrya virginiana,* the xeric *Quercus* species, and *Carya ovata.* Towards the center of the ordination the Juniperus glades merge with a series of Quercus opening stands which have a species intergradation from *Quercus ellipsoidalis-velutina* and *Quercus alba* to *Quercus macrocarpa.* Within this area, 2 species, *Quercus e.-v.* and *Q. macrocarpa* often reach exclusive dominance, while in other stands, combinations of *Quercus alba* with *Q. e.-v.* and of *Quercus e.-v.* with *Q. macrocarpa* can be expected. Secondary species, including *Betula papyrifera, Populus tremuloides, Carya ovata, Acer negundo, Prunus serotina, Quercus borealis* and *Ulmus americana,* occasionally occur within the Quercus openings. Further toward the right of the ordination in Table I, the *Quercus macrocarpa* openings grade into *Quercus bicolor-Ulmus americana* groves and into *Ulmus americana-Fraxinus pennsylvania* groves. These stands often contain 6 or more secondary species including *Carya ovata, Quercus borealis, Tilia americana, Juglans nigra, X Quercus bebbiana, X Quercus schuettii, Fraxinus americana, Ulmus rubra,* and *Carya cordiformis.* The Ulmus-Fraxinus groves intergrade toward the far right of the ordination with bottomland savanna with varying combinations of *Acer saccharinum, Betula nigra, Fraxinus pennsylvanica, Quercus bicolor,* and *Ulmus americana* as important species, and with *Tilia americana, Fraxinus americana, Ulmus rubra, Carya cordiformis* and *Fraxinus nigra* occasionally present.

The alignment of species along the ordination in Table I suggests relationship, in part, with a soil moisture-drainage regime ultimately controlled by such topographic and physiographic features as degree of slope, direction of slope facing, and surface and subsurface drainage dissection. The availability of moisture in upper soil layers was, in part, dependent on the completeness and rapidity of drainage which decreased greatly from the quickly drained Juniperus glades and other steep slope savannas to the poorly drained meadows with *Quercus bicolor, Ulmus americana* and *Fraxinus pennsylvanica* and then increased towards the better drained bottomlands. The amount of soil surface evaporation, judged by degree of exposure, decreased rapidly from the south-west and west facing Juniperus glades toward the usually level stands of the center and right of the ordination. Water retaining capacity of the soil, judged from laboratory tests using method of Partch (1949) and from depth of the A_1 layer and its organic matter content, increased from the thin soiled Juniperus glades toward the deep soiled mesic savanna in the center of the ordination and then decreased towards the frequently silted soils of the bottomlands at the right. The availability of subsurface moisture, as influenced by nearness of the water table, although not tested in the field, apparently increased toward the 2 right-most ordination intervals. Inundation is present in the right-most interval in stands dominated by *Acer saccharinum, Ulmus americana,* and *Betula nigra.* The transition in Table I is, therefore, from species most successful at 1) low surface and subsurface moisture and rapid drainage, to 2) higher surface and subsurface moisture and good drainage, to 3) high surface and subsurface moisture and poor drainage, to 4) lower surface moisture, high subsurface moisture, better drainage, and inundation.

Figures 2-5 illustrate the 4 major types of savanna community in Wisconsin. Figure 2 shows a scattering of *Juniperus virginiana* through a dry lime prairie above the Wisconsin River near Okee. Other trees in this stand are *Quercus ellipsoidalis-velutina*, and *Tilia* "xeric." Figure 3 shows a *Quercus ellipsoidalis-velutina* opening on dry-mesic prairie near Lodi; other trees include *Quercus alba* and a few *Quercus macrocarpa*. Figure 4 is of Albion Opening, near Albion, which is a stand of 200 year old *Quercus macrocarpa* on what was originally mesic prairie. A low meadow savanna with *Quercus bicolor, Q. macrocarpa*, and *Ulmus americana* is shown in Figure 5, taken near Hebron.

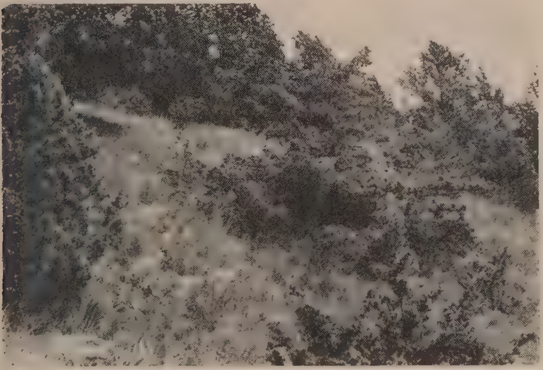
FIG. 2. *Juniperus virginiana* glade in dry-lime prairie near Okee, Wisconsin. Prominent grasses include *Andropogon scoparius, Bouteloua curtipendula, Bouteloua hirsuta*, and *Stipa spartea*. Other tree species are *Quercus ellipsoidalis-velutina* and *Q. macrocarpa*.

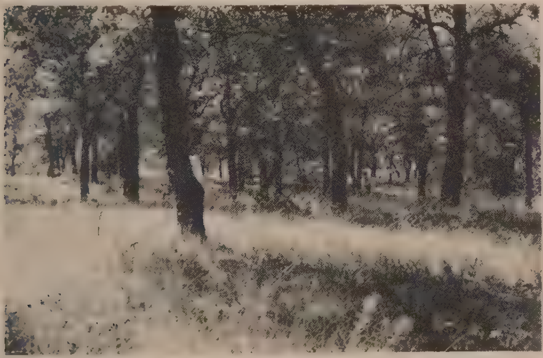
FIG. 3. Mesic dry *Quercus ellipsoidalis—velutina* opening near Lodi, Wisconsin, with *Q. macrocarpa* and *Q. alba* also present. Important understory plants include *Amorpha canescens, Andropogan scoparius, Carex pensylvanica, Poa pratensis* and *Stipa spartea*.

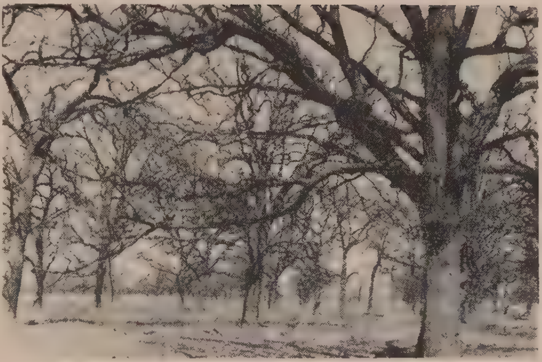
FIG. 4. Mesic Quercus opening near Albion, Wisconsin, with a pure stand of 200 + year old *Quercus macrocarpa*. Understory grazed.

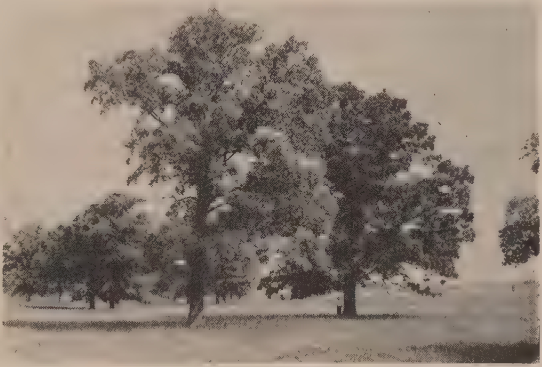
FIG. 5. Low meadow savanna near Hebron, Wisconsin, with *Quercus bicolor* in left foreground and *Q. macrocarpa* in right foreground. *Ulmus americana* is also present. Understory grazed.

Understory Composition

In 82 homogeneous stands sampled in 49 geographic locations, there was a total of 300 understory species. Table II presents all species which occurred in 10% or more of the 49 geographic locations. Per cent presence of these species in the 49 geographic stands is listed in column 2. To be counted present the species was required to occur in at least one of the sampled quadrats of the area. The fourth column of Table II gives the sum of the per cent frequencies of the species in the 82 homogeneous stands. Three species, *Euphorbia corollata, Poa pratensis* and *Amorpha canescens*, have the highest sum of frequency values and together with *Galium boreale, Amphicarpa bracteata, Rosa suffulta, Andropogon gerardi, Andropogon scoparius, Monarda fistulosa* and *Coreopsis palmata* account for one-third of the total sum of per cent frequency values. Species marked with an asterisk in column 4 are shrubs of large size which have a high basal cover per acre, not necessarily reflected by a similar high level of frequency.

Of the 113 species which occur in 20% or more of the 82 homogeneous stands, 15 are grasses or sedges, 13 are woody shrubs and 85 broad leaved

TABLE II. Understory species data and savanna ordination. "Presence" requires occurrence in sampled quadrats. The sums of frequencies (ΣF) are given for 82 "homogeneous" savanna stands

	PERCENT PRESENCE			Σ F	ADAPTATION VALUE		MEAN FREQUENCY BY SAVANNA ORDINATION INTERVALS						
	Prairie	Savanna	Forest		Prairie	Forest	2	3	4	5	6	7	8
No. of stands	59	49	60	82	—	—	8	15	14	12	7	7	11
Bouteloua hirsuta	22	12	00	141			10	01	00	00	00	00	00
Aster oblongifolius	41	10	00	70			10	02	00	00	00	00	00
Arenaria stricta	47	14	00	225			15	02	01	00	00	00	00
Aster sericeus	56	16	00	456			29	06	01	00	00	00	00
Sporobolus heterolepis	79	18	00	321			23	06	00	00	00	00	00
Andropogon scoparius	98	63	00	1499	1	1	64	27	08	01	00	00	00
Linum sulcatum	32	18	00	127			04	03	00	00	00	00	00
Bouteloua curtipendula	73	29	00	615	1	1	41	13	02	00	01	00	00
Scutellaria parvula	42	16	00	104			07	02	01	00	00	00	00
Stipa spartea	73	33	00	938	1	1	26	13	03	02	00	00	00
Koeleria cristata	25	29	00	241	1	2	10	02	03	01	00	00	00
Helianthemum canadense	03	29	00	377	2	2	20	07	05	01	00	00	00
Sorghastrum nutans	41	14	00	171			07	04	02	00	00	00	00
Petalostemum purpureum	76	43	00	1049	1	1	27	12	07	03	00	00	00
Helianthus laetiflorus	61	24	00	1034	2	1	40	26	07	04	00	00	00
Solidago nemoralis	74	37	00	466	1	1	27	08	05	02	03	00	00
Anemone patens	42	12	00	70			03	02	00	01	00	00	00
Andropogon gerardi	93	63	00	1523	2	1	52	36	15	05	01	00	00
Elymus canadensis	17	14	00	438			07	07	01	02	00	00	00
Tephrosia virginiana	03	14	00	113			03	05	01	00	00	00	00
Viola pedata	15	49	02	681	1	2	13	17	06	01	00	00	00
Aster ericoides	73	20	00	252	1	1	13	04	05	03	00	00	00
Aster linariifolius	10	16	00	128			02	06	01	00	00	00	00
Petalostemum candidum	22	24	00	333	2	2	07	08	05	00	00	00	00
Artemisia caudata	49	20	00	119	1	1	04	02	01	00	01	00	00
Oenothera biennis	24	29	00	156	1	2	05	01	03	01	00	00	00
Potentilla arguta	62	29	00	288	1	1	08	04	03	01	01	00	00
Panicum leibergii	59	37	00	528	2	1	11	11	06	02	01	00	00
Anemone cylindrica	34	49	00	853	1	2	15	08	10	03	02	00	00
Helianthus occidentalis	32	33	00	699	2	2	09	11	10	02	00	00	00
Arabis lyrata	19	16	00	91			03	02	02	00	01	00	00
Coreopsis palmata	71	49	00	1392	2	1	23	29	09	15	01	00	00
Physalis virginiana	22	41	00	316	1	2	04	04	02	01	01	00	00
Sisyrinchium campestre	49	14	00	136			02	04	01	00	01	00	00
Amorpha canescens	80	75	08	2547	1	1	55	46	13	28	10	02	00
Solidago rigida	76	22	00	388	2	1	05	06	04	03	00	00	00
Liatris aspera	57	24	00	274	2	1	03	04	05	01	00	00	00
Lithospermum canescens	54	49	00	1155	2	1	10	17	12	08	02	00	00
Euphorbia corollata	88	84	15	2684	1	1	39	42	28	33	09	04	00
Tradescantia ohiensis	24	35	02	641	3	2	06	06	15	06	00	00	00
Ambrosia artemisiifolia	54	20	02	94	1	1	04	01	02	00	03	00	00
Lespedeza capitata	16	45	00	486	2	2	02	13	05	05	02	00	00
Lobelia spicata	25	16	02	209			02	04	04	00	01	01	00
Antennaria spp.	37	61	10	818	1	2	12	10	09	06	06	03	00
Aster azureus	56	26	00	383	2	1	09	05	01	09	00	03	00
Rhus glabra	17	33	03	554*	1	2	03	09	05	01	03	01	00
Ratibida pinnata	56	31	00	822	2	1	01	11	09	08	01	00	00
Salix humilus	15	29	00	207*	3	2	02	05	04	05	01	00	00
Comandra richardsiana	59	77	05	990	2	2	07	16	10	13	07	02	00
Rudbeckia hirta	15	29	00	548	2	2	01	06	09	04	02	00	00
Krigia biflora	02	16	00	76			01	01	02	03	00	00	00
Apocynum androsaemifolium	10	51	48	908	2	2	01	08	05	16	06	10	06
Aster laevis	30	22	00	461	2	1	02	05	02	11	01	00	00
Polygonatum canaliculatum	03	45	17	209		2	02	03	03	03	01	02	00
Fragaria virginiana	12	59	42	800	3	2	00	06	08	19	08	25	05
Aquilegia canadensis	02	32	10	261			05	01	07	05	04	03	00
Bromus kalmii	02	16	00	60			00	01	03	04	00	00	00
Kuhnia eupatorioides	43	22	00	530	1	1	00	02	03	01	03	00	00
Rosa suffulta	83	69	45	1691	1	1	08	21	16	29	18	03	05
Ceanothus americanus	13	37	05	412*	2	2	01	05	07	10	01	01	00
Lathyrus venosus	00	22	00	128	3	2	01	01	02	05	03	00	00
Achillea millefolium	10	16	00	412			00	03	05	01	10	00	00
Solidago juncea	08	22	00	338		3	01	02	05	01	02	05	00
Galium boreale	06	51	28	1901	3	2	03	13	19	31	09	13	08
Monarda fistulosa	39	67	20	1323	2	2	06	19	11	25	23	18	02
Dodecatheon meadia	24	14	05	398	3		01	01	04	06	03	00	03
Aster sagittifolius	02	29	26	415		2	01	06	03	06	10	03	02
Vitis riparia	07	59	17	596*		2	01	06	05	09	13	02	02

(TABLE II. Continued)

	PERCENT PRESENCE			Σ F	ADAPTATION VALUE		MEAN FREQUENCY BY SAVANNA ORDINATION INTERVALS						
	Prairie	Savanna	Forest		Prairie	Forest	2	3	4	5	6	7	8
No. of stands	59	49	60	82	—	—	8	15	14	12	7	7	11
Helianthus strumosus	00	53	40	1290		2	01	08	10	36	13	10	06
Smilacina stellata	10	41	25	757	3	2	05	04	08	17	07	05	11
Celastrus scandens	05	31	50	820*		3	04	07	01	11	20	03	07
Heuchera richardsonii	20	20	03	132	3	2	00	01	01	02	06	00	00
Veronicastrum virginicum	05	18	22	121	3		00	01	03	01	00	04	00
Amphicarpa bracteata	00	59	60	1871		3	01	17	26	38	19	34	15
Thalictrum dasycarpum	05	10	00	354	3		00	02	03	06	01	06	01
Pycnanthemum virginianum	07	14	00	251	3		00	03	02	01	06	00	03
Potentilla simplex	00	22	38	130		3	00	02	02	02	06	02	03
Viola cucullata	00	37	55	396	3	3	01	02	04	11	05	06	09
Corylus americana	01	49	80	870*	3	3	01	12	05	29	21	29	30
Zizia aurea	04	14	12	135	3		00	00	01	04	01	06	01
Anemone quinquefolia	00	29	60	355		3	00	02	01	11	26	02	14
Solidago ulmifolia	00	16	33	664	—		00	02	01	10	05	15	05
Rhus radicans	03	43	63	541		3	01	01	02	03	11	04	10
Carex pensylvanica	00	33	58	612		3	00	04	08	14	26	36	22
Pteridium aquilinum	00	35	50	370		3	00	01	07	11	11	20	16
Desmodium glutinosum	00	37	70	787		3	00	01	06	18	11	34	16
Parthenocissus vitacea	01	45	80	362*		3	01	02	06	15	18	14	35
Rubus allegheniensis		31	48	304*		3	00	03	01	10	00	08	15
Smilacina racemosa	00	61	100	658		3	00	05	09	20	24	30	42
Cornus racemosa	00	55	80	911*		3	00	06	09	13	27	34	40
Prenanthes alba	00	35	48	158		3	00	00	02	05	02	04	09
Galium concinum	00	26	68	276		3	00	02	05	05	04	55	14
Smilax herbacea	00	24	26	178		3	00	00	00	02	07	10	03
Aralia nudicaulis	00	31	50	569		3	00	00	05	04	09	20	13
Athyrium pycnocarpon	00	06	57	30			00	00	00	02	01	01	03
Rubus strigosus	00	26	47	177*			00	01	01	03	10	13	14
Geranium maculatum	03	59	98	899	3	3	01	03	05	21	17	51	62
Sanicula gregaria	—	08	60	115			00	00	00	00	04	12	03
Botrychium virginianum	00	12	63	30			01	00	00	01	01	06	07
Vitis aestivalis	00	00	50	00			00	00	00	00	00	17	04
Adiantum pedatum	00	02	53	10			00	00	00	00	01	01	02
Phryma leptostachya	00	16	70	120			00	00	01	01	12	08	28
Circaea quadrisulcata	00	22	68	119		3	00	00	01	02	04	02	26
Osmorhiza claytoni	00	06	78	30			00	00	00	01	02	03	20
Poa pratensis		60		2612									

* Species marked with an asterisk in column 4 are shrubs of large size which often have a high basal area not reflected by level of frequency.

herbs. These species include 28 Compositae, 13 Gramineae, 10 Leguminosae, 6 Rosaceae, 6 Liliaceae and 4 Ranunculaceae. The remaining 46 species are scattered among 32 families. The distribution of savanna species by families is, therefore, fairly similar to the family distribution of prairie species. In general, savanna understory in Wisconsin contains, on a cover basis, less grass and more forbs and woody shrubs than prairie, while it contains more grass, about the same amount of woody shrubs, and fewer forbs and woody vines than forest. No species was limited in amplitude to savanna although several, including *Symphoricarpos occidentalis, Convolvulus spithameus, Wulfenia bullii, Ceanothus americanus* and *Tephrosia virginiana,* were almost so. These occurred in shrubby prairie, but were rare in closed canopy forest.

The possibility of a fairly distinct savanna association was tested by comparing the per cent presence of species within 59 prairies, 49 savannas, and 60 incipient to early intermediate upland forests in southern Wisconsin. The data for prairie and forest stands was from the vegetation files of the Ecology Laboratory of the University of Wisconsin. The result of this compilation is presented in the first 3 columns of Table II. Of the 103 species with complete data in Table II, 37 reach peak per cent presence in prairie, 36 peak in savanna and 28 in forest. The possibility of a distinct association is, therefore, doubted and the expected position of savanna as intermediate to prairie and forest is affirmed.

Because of the transitional nature of savanna composition and the wide geographic and spatial cover of savanna, the separation of a prairie or forest biotic province is extremely difficult in Wisconsin. There is no common geographic boundary of groups of plant species in the savanna region, although some species reach range limits at various places within the area. It was noted by Peters (1955) that it is usually where there are discontinuities in the environmental complex on a geographic level that a biotic province is a workable hypothesis; otherwise, there is geographic intergradation in species ranges in the same manner as there is community intergradation. The nature of the prairie-forest transition was examined, therefore, from two viewpoints: that of a spatial transition which can be sampled and often observed in the field by transect study, and that of a transition in the quantitative composition of all sampled stands.

Transect Study

The results of one transect study were presented in Bray (1956). Six additional studies were made, 3 with line transects from prairie into closed canopy forest and 3 with transects from prairie to the trunks of lone trees surrounded by prairie. Results of these two types of transects showed the same patterns of continuous interchange in composition presented in the original paper, although the two types differed in the following respects: (1) immediately beneath the canopies of lone trees there were often weeds carried by birds, such as *Asparagus officinalis* and *Solanum dulcamara*, (2) beneath lone tree canopies there was usually an absence of such pioneer forest species as *Aralia nudicaulis*, *Desmodium glutinosum*, *Lathyrus ochroleucus*, *Osmorhiza claytoni*, and *Vitis aestivalis*. Many plants which reached peak importance close to the trunks of lone trees as *Cornus racemosa*, *Galium boreale*, and *Helianthus strumosus* tended to occur away from the trunks in the more closed canopy forests and in these forests to grow in more open areas where the light intensity was the same as under the lone trees. This indicates that light intensity is more probable than interspecific association between the tree species and these plants as an explanation for their occurrence beneath lone prairie tree canopies.

Ordination Study

Along the savanna tree ordination in Table I, there is no correlation between the per cent canopy cover of a stand and its position in the ordination. Any correlation of understory composition with the tree ordination without considering tree density is, therefore, not possible, since canopy cover is a major control of understory distribution. The fortunate circumstance of the availability of forest and tree understory ordinations constructed by Gilbert (1953) and Curtis (1955) led to the possibility of showing savanna understory stands within a two-dimensional ordination. The adaptation value technique of Curtis and McIntosh (1951) was used in this ordination. Prairie adaptation values were based on Table I in Curtis (1955). All species in 10 or more of the 49 savanna geographic stands were assigned a value of 1, 2, or 3 depending on whether they reached peak per cent presence in the last 3 columns, the middle 3 columns or the first 3 columns of this table. These values are listed in column 5 of Table II. A value of one indicates tendency toward dry prairie, of 2 toward mesic prairie and of 3 toward moist prairie. Forest adaptation values were based on Gilbert (1953) and on behavior of species in the first 3 columns of Table II. These values are listed in column 6 of Table II, with a value of 1 indicating tendency toward prairie, 2 toward savanna, and 3 toward forest. For those species which peaked strongly toward forest it was not possible to assign prairie adaptation values. Both a prairie and forest ordination index were assigned to each of the 82 homogeneous understory stands by weighting the per cent frequencies in the stand by the prairie or forest adaptation values and dividing the sum of these weightings by the sum of the per cent frequencies. An additional 9 stands from the incipient end of the upland forest continuum of Curtis and McIntosh (1951) were included in the ordination.

The position of each stand along the forest ordination is shown on the X axis of Figure 6; position along the prairie ordination is shown on the Y axis of the same figure. The distribution of stands in Figure 6 suggests a linear alignment along the diagonal from a low prairie-low forest index to a high prairie-high forest index. This alignment had a highly significant correlation coefficient; therefore, a linear compression of the distribution of stands in Figure 6 seemed justified. This compression was accomplished by projecting each stand perpendicularly onto the line of the diagonal running from upper left to lower right in the figure. An ordination based on the diagonal projection from Figure 6 is given in the last 7 columns of Table II. The diagonal was divided into 8 equal intervals and the mean per cent frequency of each species calculated for the stands of each interval. The first interval of the gradient is not included in Table II since it contained only one stand. In geographic areas containing 5 or more homogeneous stands, only 3 stands were included

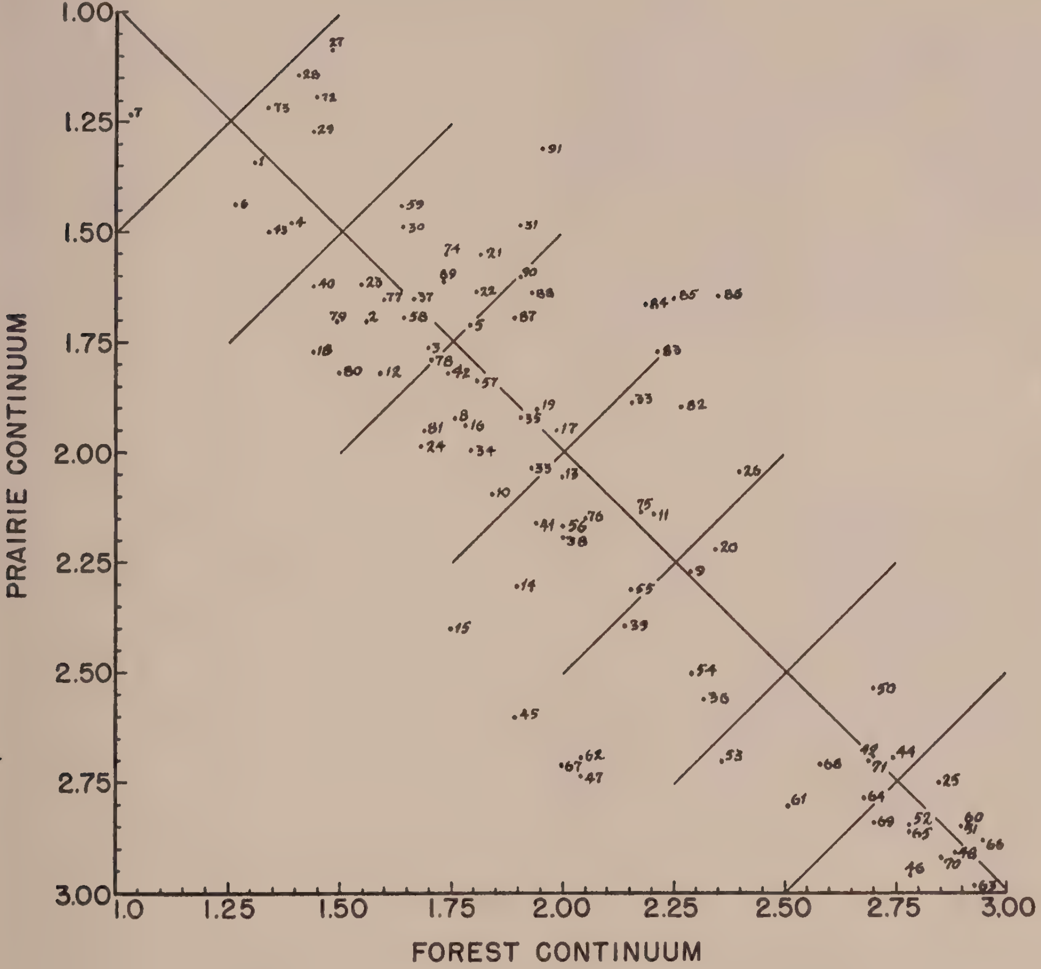

FIG. 6. A two dimensional ordination showing the location of 91 savanna and incipient forest understory stands along a Forest Continuum (X axis) and Prairie Continuum (Y axis). There is a highly significant positive correlation of stand position along each of the two axes.

in the ordination so that the area would not be given undue importance. The order of species in Table II was determined by weighting the per cent frequency values in each column of the ordination by the number of the column, summing this value, and dividing by the sum of the per cent frequencies.

As was found in the transect studies discussed above, there is a continuous interchange in species composition within the ordination in Table II. The central columns have relatively lower values than the columns at either end. This is caused by the separation of the centrally located stands in Figure 6 which results in a greater divergence in stand composition within the center of the ordination. Important species peaking towards this center include *Fragaria virginiana, Rosa suffulta, Galium boreale, Monarda fistulosa, Helianthus strumosus, Smilacina stellata* and *Amphicarpa bracteata.*

Photographs showing savanna understory for dry and mesic-dry stands are in Figures 2 and 3, for a mesic savanna near Kenosha, Wisconsin in Figure 7 and for a mesic-moist savanna near Eagle in Figure 8.

The trend of understory stands within the ordination in Figure 6 represents a transition from stands with species characteristic of high light intensities and low soil and air moistures to stands with lower light intensities and higher soil and air moistures. Although there is a spindle shaped widening toward the center of the ordination, there is an absence of stands in both the upper-right and lower-left of the figure. The lack of stands in

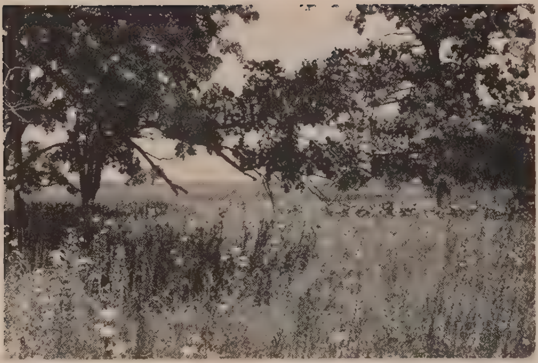

FIG. 7. A mesic *Quercus macrocarpa* opening near Kenosha, Wisconsin; Lake Michigan in background. Understory plants include *Liatris pycnostachya* and *Ratibida pinnata*.

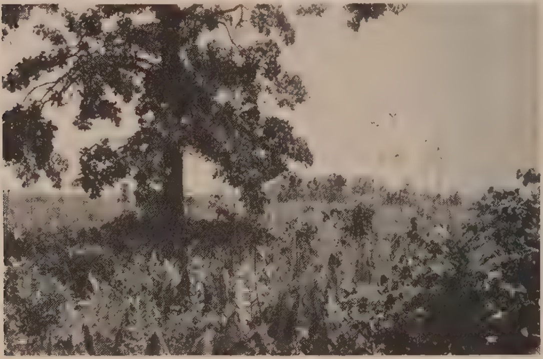

FIG. 8. A mesic-moist *Quercus macrocarpa* opening near Eagle, Wisconsin. Understory includes *Corylus americana*, *Quercus macrocarpa* seedlings and *Silphium terebinthinaceum*.

the upper-right may be due partly to the improbability of a forested habitat having low soil and air moisture conditions, since the influence of shading raises these factors. The lack of stands in the lower-left of Figure 6 apparently reflects a relationship between the positions of species in the prairie and forest ordinations. It was demonstrated by Bray (1958) that at a given soil moisture level, as shading increases, the understory species include increasingly those of the more mesic and moist levels of the prairie continuum. That is, if tree shading occurs in a xeric prairie, the species beneath the tree canopies will be increasingly those of mesic prairie, while if shading occurs in a mesic prairie, the species beneath tree canopies will be increasingly those of moist prairie. The dry prairie species (values of 1) should have low forest adaptation values, therefore, because of their low shade tolerance; while species which peak toward "mesic" and "moist" prairie continuum intervals (values of 2 and 3) should have higher forest adaptation values. An examination of the prairie and forest adaptation values in columns 5 and 6 of Table II shows this is the case. The values are highly correlated; in 25 of 49 instances they are identical, and in no instance are they separated by a factor of 2. This correlation of adaptation values prevents stands from occurring in the lower-left or upper-right of Figure 6 and determines the linear tendency of the ordination.

As shading from forest trees increases in a prairie at any level of the prairie continuum, there is, therefore, a gradual shift to species of the moister prairie continuum intervals and to species more characteristic of forest. In this transition, prairie species with abundant stored food in roots or rhizomes, as *Cacalia tuberosa, Dodecatheon meadia, Saxifraga pennsylvanica,* and *Silphium terebinthinaceum* may survive for a long period, but their vitality declines and they contribute little to the above-ground cover. The mechanisms which underly the light-moisture relationship noted here should be investigated. The distribution of prairie species along a soil moisture gradient is, in part, determined by the devices which species have evolved to prevent excessive evaporation. The dry prairie species are mainly those which have the necessary adaptations to prevent excessive water loss, as epidermal hairs, wax coatings, and thickened cuticle and epidermal layers. However, such devices may at the same time reduce light penetration to the photosynthetic tissue, thus leaving the xerophyte species at a disadvantage under shading since their photosynthetic tissues would receive too little light to successfully compete with the more mesic species.

Although there were no understory data for the grazed savanna stands, it is possible to predict the joint tree and understory composition by a synthesis of information in Tables I and II. In general, the further a tree community is towards the right-most intervals of the ordination in Table I (excluding bottomlands which are complicated by inundation) and the more dense its canopy, the more likely its species composition will be towards the right-most intervals of the ordination in Table II; the further the tree composition is towards the left of Table I and the less dense its cover, the further its understory will be towards the left of Table II. Thus, the range of understories in a *Quercus ellipsoidalis-velutina* opening would be further toward the left part of the understory ordination at a given density than the combination possible for a more mesic *Quercus macrocarpa* stand, and the *Quercus e.-v.* opening would have, at a higher amount of canopy cover and shading, the understory found in a *Quercus macrocarpa* opening at a somewhat lower amount of shading. A great diversity of composition is, therefore, possible.

Relationship with Soil Features

There was a tendency for some savanna communities to be prevalent on a limited number of soil types, but this was usually coincidental. Thus, *Juniperus virginiana* glades usually occur on fine sandy to sandy loam soils which have a high calcium content. This occurrence is related to past geologic coincidences, however, as most areas in Wisconsin which are bluffy or steep enough to protect Juniperus from fire have a parent material of limestone or limey standstone, or of limey loess which lies on quartzite rocks. The original predominance of *Quercus macrocarpa* on flat land deeply humic soils and the higher prevalence of *Quercus velutina* and *Quercus alba* savanna on the thinner leached soils of medium to steep slopes is related, in part, to historic disturbance factors which limited *Quercus velutina* and *Q. alba* to slopes (except on sand) and allowed *Quercus macrocarpa* to invade some prairie flatlands.

The relation of savanna vegetation to some soil features of the A_1 layer is shown in Table III.

Table III. Soil data summary. Mineral concentrations are expressed in 10's of pounds per acre, at two depths

	Ordination Interval				
		Savanna			Forest
	Prairie	0-.33	.34-.66	.67-1.0	2400-2700
Number of stands	51	10	19	5	3
Soil pH per 7 in. depth	—	7.1	5.9	5.3	7.0
Minerals per 7 in. depth					
Calcium	815	670	590	190	865
Magnesium	95	105	71	28	51
Phosphorus	11	13	5	3	6
Potassium	23	22	20	8	17
Minerals in the A_1 horizon					
Calcium	—	310	130	75	520
Magnesium	—	16	17	14	28
Phosphorus	—	0.8	1.2	0.9	3.8
Potassium	—	4.3	5.3	2.6	10.5

The 2nd through 4th columns of the table list mean averages for the stands along the understory gradient in Table II, as divided into 3 equal sections. The included stands occurred only from the interval 1.0 to 3.0 of the tree ordination in Table I since the stands of the more moist intervals were grazed and consequently the soils were disturbed. To show the comparative relation of savanna soils to those of prairie and forest, prairie data are listed from Curtis (1955) in column 1 and forest data from the files of the Ecology Laboratory of the University of Wisconsin are in column 5. The forest soil data list mean characteristics for stands in the interval 2400-2700 of the southern upland forest continuum (Curtis and McIntosh 1951). A transition is available in Table III, therefore, from prairie through intervening savanna of an increasing tree density to a near-terminal forest.

The values in the first section of Table III represent mean fertility in 10's of pounds per acre for a soil depth of 7 in. Ca, Mg, P, and K decrease in magnitude from prairie in column 1 to the dense savanna in column 4 dominated by *Quercus ellipsoidalis-velutina* and *Q. alba* and then sharply increase toward the 2400-2700 near terminal forest interval in column 5. The initial decrease reflects, in part, the age of the soils, since soils toward the left tend to be younger. Many of the stands in the first and second columns occurred on steep slopes on which the parent limestone or limey standstone was close to the surface. The steepness of these slopes, some of which were over 45°, contributed to a slight sheet erosion, and the soil beneath the usually thin organic layer often contained small pieces of undecomposed rock. The decreasing nutrient level within the savanna and subsequent closed canopy forest is probably caused by the increasing density of Quercus per acre. It has been shown (Lutz and Chandler 1946, Coile 1937) that the calcium content of fallen leaves is lower for most species of Quercus than for most other hardwood species (mean calcium per cent *Quercus velutina,* 1.1; *Quercus alba,* 1.4; *Acer saccharum,* 1.8; *Carya cordiformis,* 3.4; *Tilia americana,* 3.8). Although the pumping of Mg, K, P, and N of *Quercus velutina* and *Q. alba* is approximately the same as for *Acer saccharum* or *Tilia americana,* the buffer systems in the Quercus leaves, perhaps because of the lower Ca content, do not buffer the soil enough as they decompose to prevent leaching. A further explanation for decreasing nutrient levels in Quercus forest is that the Quercus leaves, because of their lower Ca content, decompose slowly and some leaves are likely to be blown away and the contained minerals lost. This loss is especially prevalent in stands on steep slopes or bluff edges where there is often a complete absence of litter and only a thin humus layer. The downward trend in nutrient content in columns 1 through 4 is reversed as lime pumping trees replace Quercus. In the 2400-2700 interval of Table III, in forest dominated by *Acer saccharum, Tilia americana, Carya cordiformis* and

Ulmus rubra, pH has again reached neutrality and higher levels of Ca, Mg, P, and K are present.

The second part of Table III lists nutrient values per A_1 per stand. The higher values of Mg, P, and K toward the intermediate interval (.34-.66) are caused by the deeper soils in this interval compensating for the lower nutrient content per unit volume. The soils in the first interval were shallow and from steep slopes, since the more deep soil savannas were grazed and soil samples were, therefore, not collected. Minimum nutrient levels are again found, however, in the interval of dense savanna (.67-1.00) in column 4.

The values in column 5 of Table III contain a high standard error (1380 for Ca part one) in relation to the mean. Given this high value, however, the trend from column 4 to 5 is still reliable. The values from the 3 savanna intervals contain smaller standard errors (1,240, 1,002, and 1,360 for Ca) and the trend from the higher nutrient values in columns 2 and 3 to the lower values in column 4 is reliable.

The demonstration in Table III of a similar magnitude in level of fertility in prairie and in near terminal forest supports the steady state or dynamic equilibrium concept discussed by Nikiforoff (1942, 1959). The independence of time of this equilibrium is strongly emphasized in these studies.

SUMMARY

1. The composition of Wisconsin savanna communities in which open grown trees were scattered through grassland was sampled with 60 tree stands and 82 understory stands. Tree stands were surveyed with the random pairs method; understory stands with a total of 1760 1 x 1 m quadrats. Measurements of light intensity and collections and analysis of the A_1 soil horizon were made.

2. The major savanna communities in Wisconsin are Juniperus glades, Quercus openings and Ulmus-Fraxinus groves. Six tree species, *Juniperus virginiana, Quercus ellipsoidalis-velutina, Q. alba, Q. macrocarpa, Q. bicolor,* and *Ulmus americana* accounted for 90% of the sum of importance values. A linear ordination of the tree stands was made, using the adaptation value technique, with a resulting order of major species as listed above. This ordination appeared correlated, in part, with a soil moisture and drainage regime.

3. Three hundred species of herbs and shrubs were found in savanna, of which *Euphorbia corollata, Poa pratensis, Amorpha canescens, Galium boreale, Amphicarpa bracteata, Rosa suffulta, Andropogon gerardi, Andropogon scoparius, Monarda fistulosa,* and *Coreopsis palmata* contributed one-third of the total sum of frequency values. The intermediate position of savanna understory composition was emphasized in a comparison with prairie and forest stands.

4. The understory stands were ordered, using the adaptation value technique, within a previously constructed prairie continuum which was correlated with a dry to moist soil regime, and along a forest gradient representing increasing degree of shading. This two-dimensional ordination showed a highly significant linear alignment of the stands which was the result of a tendency for species peaking in "dry" prairie to be the least shade tolerant and for "moist" prairie species to be the most shade tolerant.

5. Analysis of chemical features of savanna soils indicated a decrease in Ca, Mg, K, P, and pH as the savanna soils aged and the canopy closed with an increasing density of Quercus and of Quercus litter.

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ECOLOGICAL SIGNIFICANCE OF SEED COAT IMPERMEABILITY TO MOISTURE IN CRIMSON, SUBTERREANEAN AND ROSE CLOVERS IN A MEDITERRANEAN-TYPE CLIMATE

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From an evolutionary point of view, impermeability of the seed coat to moisture is a valuable characteristic for continuance of a plant species under conditions of climatic adversity. Not only do impermeable seeds remain viable for a long time, but under natural conditions increments of a seed population become permeable to water and germinate in successive intervals. Hence, seed produced in a favorable season is often capable of producing seedlings over many years, providing numerous opportunities for species survival.

This consideration is also of ecological significance in stands of winter annual clovers seeded on rangeland. A much desired objective is a permanent stand of legumes after the initial seeding effort, and the production of impermeable seeds is important for legume survival on California ranges. The timeliness and amount of precipitation received are vital factors to stand establishment on such rangeland. After sufficient moisture in autumn to germinate seeds of winter annual species, subsequent drought often causes seedling mortality. If an annual plant has produced some impermeable seeds which become permeable over a period of time, the opportunity for the establishment of a good stand is greatly enhanced. Often the favorable circumstances of seeding can not be attained again for a number of years. This makes short-term improvements of questionable value and emphasizes the desirability of permanence in the changes brought about by vegetation manipulation.

Since seed coat impermeability is important to legume survival on rangeland, information concerning its occurrence in the clover species commonly used in seeding and the way it is influenced by environmental factors is worthwhile. Consequently, research was initiated to study the following aspects: a) the amount of impermeable seed produced by the winter annual species, crimson, subterranean and rose clovers (*Trifolium incarnatum*, *T. subterraneum* and *T. hirtum*), under dryland conditions in California, b) the rate at which seeds become permeable, and c) some factors causing breakdown of impermeability of rose clover, a species with a high degree of seed coat impermeability.

Literature Review

Most investigators of seed coat impermeability have agreed that the thickened ends of the columnar cells(i.e. Malpighian cells) of the seed coat, immediately below the cuticle, block the intake of water by impermeable seed. The testae of both impermeable and permeable seeds show the same general organization. The functional difference is due only to permeability in various sections of the seed coat of the permeable seeds. A seed which has dried moderately, but has not become impermeable, is permeable in one or more irregular patches over the coat, generally at or near the hilum. This permeability is due to incomplete formation of the suberin layer in the Malpighian cell caps of those areas. Such seeds may become impermeable by further drying, which induces continuity of the impermeable layer (Aitken 1939). Water intake by naturally permeable seeds also may occur in an unsuberized area of the strophiole (Hamly 1932).

Probably all commercially important leguminous species in the United States produce some impermeable seeds with the exception of the peanut (*Arachis hypogea*) (Harrington 1916). At the other extreme, Stevenson (1937) collected mature seed from 10,982 single plants of white sweet clover (*Melilotus alba*) and found that more than 99% of the seed was impermeable.

Factors affecting the production of impermeable seeds by legumes have been studied by many research workers. The stage of maturity of seeds has been shown to influence impermeability in legumes. Brown (1955) found that the impermeable seed percentage of broadleaf birdsfoot trefoil (*Lotus corniculatus*) increased with increasing maturity until full size of the seed was attained. Hills (1942) reported that delaying harvest up to 6 wk after the normal stage of maturity with subterranean clover caused a considerable reduction in the percentage of hard seeds. In subterranean clover, Hills (1944) also concluded that seed coat impermeability is not a major varietal character.

Aitken (1939) found that the moisture content of seed of subterranean clover was important in the formation of impermeable seed. As the seeds became drier on the plant, the percentage of impermeable seed increased. Hard seed formation also appears to be associated with the dehydration processes which may take place independently of the plant. Hyde (1954) states that the moisture content of seeds of white clover (*Trifolium repens*), red clover (*T. pratense*), and *lupine* (*Lupinus arboreus*) fell rapidly to approximately 25% (dry-weight basis), and thereafter, more slowly until the epidermis became impermeable at 14% moisture content. Further drying of the seed took place only by diffusion of water through the hilum which acted as a hygroscopically-activated valve. When the relative humidity was low a fissure in the hilum opened, permitting the seed to dry out; when the relative humidity was high the fissure closed, obstructing the absorption of moisture. Thus, the impermeable seeds tend to have a moisture content in equilibrium with the lowest relative humidity to which they have been exposed. The duration of the impermeable condition increases with the degree of dessication brought about by loss of water through the hilum.

Impermeable seeds are capable of germination, for the most part, after a treatment that makes the seed coat permeable to water. Under field conditions extremes of temperature, soil acids, soil organisms, and animal trampling and ingestion are agencies suspected of causing permeability. Permeability can be achieved artificially by mechanical scarification, impaction, chemical treatment, freezing and thawing, boiling water, or dry heat. Mechanical scarification is commonly accomplished to a greater or lesser degree in the threshing and cleaning operations where seed is produced commercially (Lute 1928). Scarification can also be accomplished in hand harvested samples by rubbing with sandpaper or notching with a file. Mechanical scarification physically breaches the impermeable layer in the seed coat allowing water to enter.

Mechanical impaction has been used successfully as a technique for reducing impermeability (Barton 1947, Brown 1955, and Hutton and Porter 1937). Hamly (1932) working with white sweet clover and Aitken (1939) with subterranean clover found that impaction caused a cleft through the strophiole of previously impermeable seed through which water could pass.

Treatment with heat or cold may also cause a splitting of the impermeable layer. Busse (1930) found that cooling to —80°C caused most of the impermeable seeds of alfalfa (*Medicago sativa*) to become permeable, but had very little effect upon impermeable seeds of sweet clover. Martin (1945) reported that impermeable seeds of sweet clover, in natural field seedlings and when stored over-winter in unheated buildings in Iowa, became 80-100% permeable by the middle of the following April. Hutton and Porter (1937), Lute (1928), Rincker (1954), Staker (1925) and Stewart (1926) found that subjecting seeds of impermeable species to dry heat temperature of 60°-85°C for periods of 2-6 hr effectively decreased the percentage of impermeable seeds. Stone and Juhren (1951) found that the fire induced germination of *Rhus ovata,* a non-legume, was the result of high temperature exposures. They concluded that a temperature of 60°C, which is often reached at the ¼ in. soil depth on exposed sites for several hours daily during the summer in many parts of California, is adequate to rupture the seed coat and induce germination.

Scarification with chemicals has also been used to reduce impermeability in certain legumes. Barton (1947) found that the subfamilies of the Leguminosae varied in their reaction to soaking in absolute ethyl alcohol for 72 hr. Impermeable seeds of the members of the *Papilionoideae* (*Cladastris, Cytisus, Melilouts,* and *Robinia*) were unaffected by the alcohol treatment. Impermeable seeds of members of the *Caesalpinoideae* (*Cassia, Cercidium, Gleditsia, Gymnocladus, Parkinsonia,* and *Cercis*) were made permeable by the alcohol soaking. Jones (1928) found that the impermeability of vetch seed (*Vicia villosa*) was not affected by immersion in ether, but disappeared upon short exposure to concentrated sulfuric acid. Burns (1959), working with blue lupine (*Lupinus angustifolius*), found that scarification with sulfuric acid rendered impermeable seeds permeable and that water then entered either through the hilar fissure or through pits eroded through the testa. Acid scarification did not permit water entry through the strophiolar area, however.

Went (1957) and his coworkers have detected a number of other adaptive mechanisms by which non-leguminous annual species of the California deserts avoid germination until conditions are favorable to their establishment. Some examples are water soluble germination inhibitors in seeds or in seed coats, inhibition by salinity, and slow water uptake by encasing structures. The effectiveness of these mechanisms of delayed germination are dependent largely on the coincidence of appropriate temperature and intensity and duration of rain.

PROCEDURE

Seeds of 3 introduced species of *Trifolium* were collected at monthly intervals in 1958 and early

1959 from several locations for determination of impermeable-seed and germination percentages. The crimson clover (*Trifolium incarnatum*) seeds sampled in this study were probably of the common or Dixie varieties although evidence for varietal identification was inconclusive. The subterranean clover (*T. subterraneum*) was of the Mt. Barker variety at all locations except the Yolo site which was observed to have a mixture of 45% Mt. Barker and 55% Tallarook varieties. The rose clover (*T. hirtum*) was of the strain selected and developed by Love and Sumner (1952) from an introduction from Turkey which has been used extensively in California range plantings since 1950.

Tests to compare the scarifying effects of the threshing method with hand removal of seed from the calyx were conducted on samples of rose clover. Seed used in the tests was hand harvested on July 8, 1958 from standing plants grown on the University Farm. Unhulled seed was placed in a corrugated rubber-lined box and rubbed with a block of wood which was covered with corrugated rubber. Hand threshing was accomplished by rubbing unhulled seed between the palms of the hands. Eight replications of 100 seeds each of both of the threshing methods were laboratory germinated. It was found that seed threshing by rubbing with a corrugated rubber-covered block of wood in a corrugated rubber-lined box gave impermeable seed percentages not significantly different from seed which was hand removed from the calyx (98 and 96% respectively). Thereafter, all seed was threshed in the corrugated rubber-lined box.

Preliminary germination tests were performed to determine the most effective temperature for the germination trials to be conducted on field seed collections. Four temperatures were tried: 10, 15, 20 and 25°C on commercial seed samples. Groups of 100 seeds replicated 4 times were germinated in the dark in covered petri dishes on Whatman No. 3 filter paper moistened with distilled water. The criterion of germination was the appearance of a sound radicle. Of the temperatures studied 15°C did not reduce the germination of any of the 3 species in comparison with the other favorable temperatures, and it had the advantage of inhibiting the growth of molds. All field collections were germinated soon after collection at 15°C in the manner described above. Storage prior to testing was at room temperature in envelopes. Germination counts were made on the third and seventh days for rose clover and crimson clover and on the fourth and fourteenth days for subterranean clover.

CLIMATE, SOILS AND VEGETATION

Seed collections were made on sites located on terraces and foothills peripheral to the Sacramento Valley of California. The climate is of the Mediterranean type or dry-summer subtropical (Köppen's Cs) and has the following characteristics: (a) precipitation occurring mainly in the winter with summers essentially rainless and (b) temperatures mild in winter and warm to hot in summer (Trewartha 1954). Collection sites in Napa and Solano Counties qualify as marine locations with cool summers (Csb) being close to San Francisco Bay. Collection sites in the 3 counties, Placer, Sacramento and Yolo, are interior locations (Csa) with hot, intensely-sunny summer days (Kesseli 1942). A monthly climatic summary for the years 1957-58 and 1958-59 when the study was in progress is in Figure 1 for 5 weather stations representing the collection sites (U. S. Department of Commerce, Weather Bureau 1957-1959).

The distance of each site from the most representative weather station, the soil type, and the age of the clover stand is indicated in Table I. All sites were between sea level and 300 ft elevation.

TABLE I. Location, soil type, and age of clover stand at collection sites.

Site location	Distance from weather station	Soil type	Age of stand in years
Napa Co.	6 mi. SW Napa	Denverton adobe clay	8*, 3**
Solano Co.	12 mi. SE Fairfield	Antioch fine sandy loam	4
Placer Co.	10 mi. NNW Rocklin	Placentia gravelly loam	6
Sacramento Co.	11 mi. ESE Sacramento	Redding gravelly loam	5
Yolo Co.—			
Rominger farm.	14 mi. NW Davis	Hartley gravelly loam	4
Mast farm	16 mi. NW Davis	Corning complex	6
University farm	2 mi. NW Davis	Zamora clay loam	2

* Subterranean clover.
** Crimson and rose clovers.

The resident vegetation is of the annual grassland type dominated by *Avena fatua, Bromus mollis, Festuca megalura, Hordeum leporinum* and *Erodium botrys* with scattered individuals of *Quercus*. Relict areas of Pacific Bunchgrass typified by *Stipa pulchra* occur near the 2 sites under a marine influence (Napa and Solano). Introduction of one or more of the winter annual clovers into the resident sward has been accomplished at each of the collection sites. The planting of annual legumes for the improvement of grazing is now a widely accepted practice for the California annual-range type. Forage production is often increased 3 or more times as a result of seeding legumes, along with suitable fertilization and grazing management (Williams et al. 1956 and 1957).

Results and Discussion

The ecological significance of seed coat impermeability relative to survival of annual leguminous species involves 4 major considerations a) the production of impermeable seeds, b) the rate at which these seeds become permeable, c) the degree of confluence of environmental factors favorable to germination and breakdown of impermeability, and d) the survival and productivity of plants developing from impermeable seed after delayed germination.

Production of Impermeable Seeds

Seeds of 3 annual clovers, used for planting rangeland in California, were collected for determinations of impermeable seed and germination percentages. Crimson and subterranean clover seeds were obtained on 5 ranches representative of foothill and valley rangeland of northern California. Rose clover seed was also collected from these ranches and 2 additional ones. The seed of all 3 species had matured by June 9, 1958 when collecting was begun. Seed collections were made of the 3 species at approximately monthly intervals through the rainless summer and autumn, and for rose clover into the winter season. Crimson and rose clover seeds were collected from plants, except where noted otherwise, and subterranean clover seed was collected from the soil surface.

Crimson clover.—The impermeable seed content of crimson clover ranged from 25-90% in the seed harvested from the various sites in June (Table II). Germination varied in a converse fashion from 74-10% in the June harvested seed, the remainder being nonviable. The impermeable seed content of crimson clover declined rapidly at all locations during the summer months. By the time of last collection date, seed from one location contained 9% impermeable seed, and the remaining locations 3% or less. Thus by November, the usual month of emergence for winter annual clovers in this region, very little impermeable seed of crimson clover remained.

Germination percentage of crimson clover increased for seed harvested during the summer months, reaching a plateau between 78 and 94% at the interior sites (Placer, Sacramento and Yolo). After a similar initial increase the crimson clover germination percentage declined from 62 and 70% by the August harvest to 34 and 42%, respectively, in the autumn for the 2 sites under a marine influence (Napa and Solano). In the September and subsequent collections most of the seed collected was from the basal portions of the crimson clover heads since the seed higher on the inflorescence had fallen. It was noted that some of these seeds were a brick-red color, which is not the normal seed color in crimson clover. These seeds were not viable. The increase in the amount of nonviable seed in the September and subsequent harvests is probably due to this factor.

The varying percentages of impermeable seed from the June harvest are probably the result of varying degrees of maturity. Slow maturity in some of the seed lots was due to more effective late moisture. Precipitation received in May and June 1958 was highest at the weather station near the Napa collection site which produced the highest impermeable seed percentage (Fig. 1).

As the seed became fully mature, impermeable seed percentages were reduced to very low levels. Lack of prsistence of seed coat impermeability in crimson clover may explain why the species does not persist on the drier sites over extended periods of time. If moisture conditions do not allow for stand establishment after germination begins, there apparently is little or no reservoir of previously impermeable seed to germinate and establish new stands when moisture conditions improve.

Subterranean clover.—Samples of subterranean clover seed from the 5 locations ranged from 58-91% impereable seed for the June collection, and germination varied from 28-9% (Table II). Seed from the later collection dates decreased in impermeable seed percentage and increased in germination percentage. By October collections from 4 locations had impermeable seed contents of 0-3% and germination percentages of 96-99%, but the seed collected from the Napa site had an impermeable seed content of 30% and germination percentage of 68% as late as December. The subterranean clover at the Napa site reached a plateau of impermeable seed values early in the autumn. This is accounted for by a later date of maturity than for the other sites. Some immature burs were observed in June at the Napa site, although these were not included in the sample collected. The delayed maturity may be attributed to the greater availability of moisture during the seed maturation period at that site (Fig. 1).

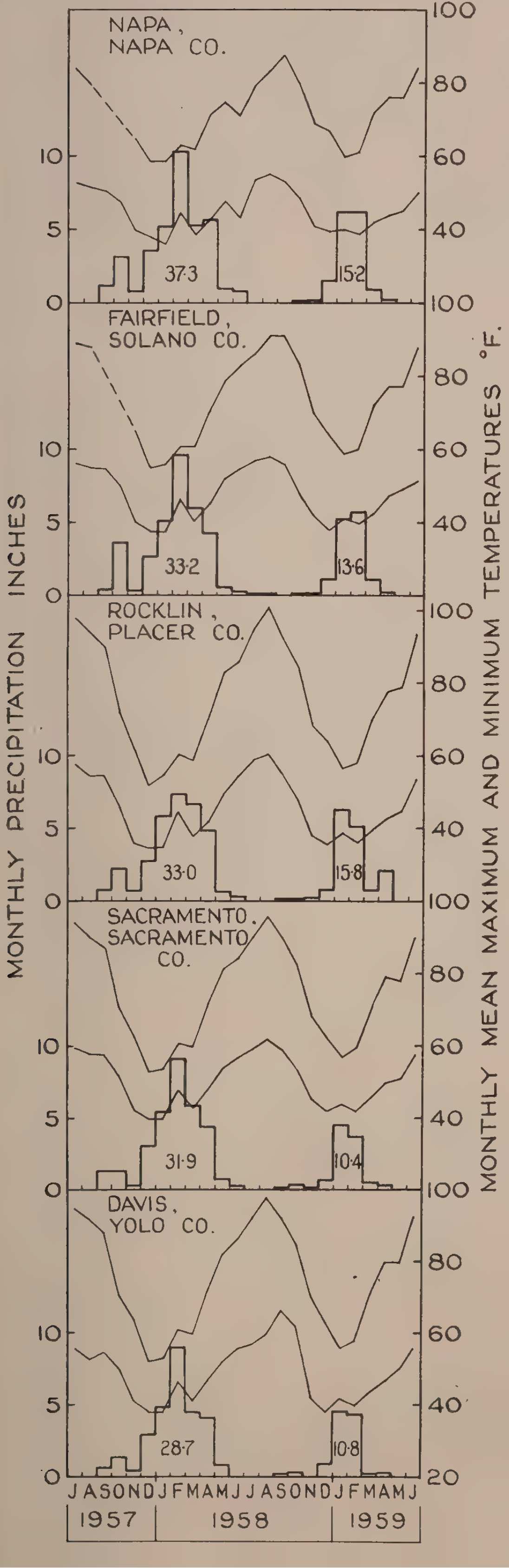

Fig. 1. Monthly precipitation and temperature data from weather stations representative of the seed collection sites.

On the whole, subterranean clover and crimson clover behaved similarly in regard to their seed coat impermeability with a rather rapid decline during the summer. However, the inception of the decline of impermeable seed content of subterranean clover was about one month later than in crimson clover. With the exception of the Napa site, the net result by October was substantially the same: a very low impermeable seed percentage.

These results are in accord with those reported for 4 varieties of subterranean clover by Donald (1959) that 90% or more of the viable seed produced in any one season germinated in the following year. He showed that the impermeable remainder was carried over and germinated in subsequent years in a logarithmically decreasing manner.

Rose clover.—Collections of rose clover seed were made for 7 to 9 months at 7 locations (Table II). The mean impermeable seed content for all times and locations was 96% with a range of 88-100%. Thus the incidence of seed coat impermeability of rose clover is markedly greater than that of the crimson and subterranean clovers. The variation in amount of impermeable seed in rose clover appeared to occur at random, and hence, no trend is evident with regard to location or time of harvest.

It is evident that rose clover seeds develop an impermeable seed coat early in the process of maturing and that impermeability is not reduced significantly during the subsequent growing season in seed remaining attached to dry standing plants.

To learn the effect on seed coat impermeability of contact with the soil surface, such as occurs following shattering of the mature inflorescences, quadrats of rose clover were hand clipped on the University Farm on July 30, 1958. Many seed-containing calyces dropped to the soil surface as a result of the plant disturbance. Subsequently, seed was collected at monthly intervals from standing plants and from the soil surface. A reduction in impermeability to 50% and a corresponding increase in germination to 49% was measured 10 wk after seed shatter occurred (Table III). In comparison, seed remaining attached to standing plants continued to have a high level of impermeable seed throughout the measurement period.

Microclimate of Mature Rose Clover Seed

Temperature is one factor known to affect the impermeability of seeds. The temperatures to

TABLE II. Effect of duration of field exposure on seed coat impermeability and germination of crimson, subterranean and rose clovers

Location	Sampling date	CRIMSON CLOVER		SUBTERRANEAN CLOVER		ROSE CLOVER	
		Impermeable %	Germination %	Impermeable %	Germination %	Impermeable %	Germination %
Napa Co.	June 13, 1958	90	10	84	15	94	5
	July 10	63	32	85	14	93	5
	Aug. 12	20	62	70	28	96	2
	Sept. 10	30	46	41	59	97	2
	Oct. 11	2	42	38	61	97	2
	Nov. 7	—	—	29	71	99	0
	Dec. 5	—	—	30	68	100	0
Solano Co.	June 10	74	23	91	9	92	6
	July 10	53	44	68	32	97	3
	Aug. 11	22	70	16	84	97	2
	Sept. 10	18	61	8	92	92	8
	Oct. 11	16	50	1	99	100	0
	Nov. 7	3	34	1	99	98	1
	Dec. 5	—	—	—	—	99	0
	Jan. 16	—	—	—	—	99	1
Placer Co.	June 9	25	74	70	28	97	3
	July 9	12	85	77	23	95	2
	Aug. 11	4	91	26	74	94	4
	Sept. 9	2	88	5	94	96	3
	Oct. 10	1	81	3	96	97	3
	Nov. 7	—	—	—	—	100	0
	Dec. 5	—	—	—	—	100	0
	Jan. 16	—	—	—	—	100	0
Sacramento Co.	June 9	40	60	58	24	88	10
	July 9	14	85	52	28	97	2
	Aug. 11	3	94	10	88	94	3
	Sept. 9	2	86	5	94	95	5
	Oct. 10	1	86	0	97	96	4
	Nov. 7	—	—	—	—	99	1
	Dec. 5	—	—	—	—	100	0
Yolo Co. Rominger	June 10	72	27	74	26	98	2
	July 10	42	58	62	37	99	1
	Aug. 12	18	78	24	75	98	2
	Sept. 9	9	78	10	88	98	1
	Oct. 10	9	78	0	99	90	9
	Nov. 6	—	—	—	—	100	0
	Dec. 4	—	—	—	—	94	6
Yolo Co. Mast	June 10	—	—	—	—	98	1
	July 10	—	—	—	—	99	1
	Aug. 12	—	—	—	—	98	1
	Sept. 9	—	—	—	—	98	2
	Oct. 10	—	—	—	—	98	2
	Nov. 6	—	—	—	—	98	2
	Dec. 4	—	—	—	—	98	2
	Jan. 16	—	—	—	—	100	0
	Feb. 25	—	—	—	—	100	0
Yolo Co. University Farm	June 11	—	—	—	—	97	2
	July 8	—	—	—	—	95	4
	Aug. 12	—	—	—	—	93	6
	Sept. 10	—	—	—	—	88	10
	Oct. 11	—	—	—	—	92	8
	Nov. 6	—	—	—	—	96	4
	Dec. 4	—	—	—	—	93	6
	Jan. 16	—	—	—	—	94	6
	Feb. 25	—	—	—	—	94	6

TABLE III. Effect of seed position on seed coat impermeability, in place on standing plants vs. shattered to soil surface, University Farm

Sampling date	IN PLACE ON STANDING PLANTS		SHATTERED TO SOIL SURFACE ON JULY 30	
	Impermeable %	Germination %	Impermeable %	Germination %
September 10	88	10	79*	20*
October 11	92	8	50*	49*
November 6	96	4	63*	36*
December 4	93	6	55*	44*

* Odds are greater than 99:1 that the value for shattered seed differs from the corresponding value for seed from standing plants.

which rose clover seed may be subjected on hot summer days were measured in a plot of rose clover on the University Farm. Temperature readings were obtained with a potentiometer and 20 microthermocouples. Readings were made in the calyces of rose clover placed on the soil surface, in the heads of dried clover plants approximately 6 in. above the soil surface, and in the air 12 in. above a bare soil surface in shade. All readings except air temperature readings were replicated 4 times. Air temperature readings were in duplicate and checked against a calibrated thermograph.

Readings taken on August 6, 1958 may be considered typical for a hot summer day. Temperatures as high as 140°F (60°C) were encountered inside rose clover calyces lying on the surface of the soil (Fig. 2). Temperatures approaching this value also occurred in clover heads 6 in. (15 cm) above the soil surface. The maximum temperature recorded by the Davis weather station on that day was 104°F (40°C). This temperature is not an unusual maximum at the sites in the interior valley (Csa). In 1958 temperatures of 104°F or greater occurred on 16 days at Rocklin, 3 days at Davis, 1 day at Sacramento, 0 days at Fairfield, and 0 days at Napa. Absolute maximums were 108, 107, 104, 100 and 101°F at the respective sites in 1958.

Cool Season Experiments

Field planting of impermeable rose clover seed.—Seed of rose clover collected from the University Farm in June 1958 was subjected to conditions favorable to germination in the laboratory and the impermeable fraction retained for further testing. Four plots 3 ft square were planted with 100 impermeable seeds each on October 31, 1958, prior to the first effective autumn rain. After the seeds were broadcast and raked in, the plots were enclosed with one in. poultry netting to exclude birds and rabbits. Counts of emerged seedlings were made at 15 day intervals from November 15, 1958 to April 15, 1959 when the soil moisture about the seeds was exhausted. A few seedlings

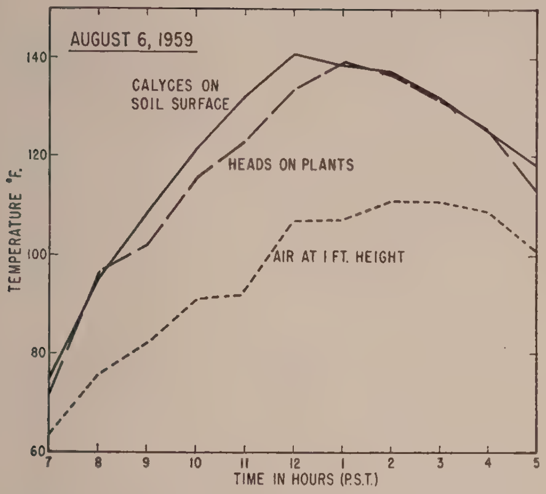

FIG. 2. Temperatures in rose clover calyces and heads on a typically hot summer day in the Sacramento Valley, California.

emerged in January and February, the total for the season being 2.4%. Thus, soil contact under a natural climatic regimen during the mild winter of 1958-59 did not result in the germination of a substantial number of impermeable seeds.

Field exposure of impermeable rose clover seed.—To observe the effect of winter climatic conditions exclusive of soil factors, impermeable rose clover seeds were placed in lots of 400 in plastic mesh bags and laid on a bare soil surface in the field, exposed to the weather, beginning October 1, 1958. Quadruplicate samples of 100 seeds each were drawn at monthly intervals and germinated in the laboratory. The percentage germination for the various periods of exposure were 1 month—1.75%, 2 months—0.75%, 3 months—2.50%, 4 months—3.50%, 5 months—2.25%, and 6 months—0.25%. The above values are net percentages and, therefore, should not be accumulated. The variation would seem to be accounted for by random sampling. The results are essentially the same as those for the field planted impermeable seeds.

Thus the climatic environment during the 1958-59 cool season at Davis, just below and above the soil surface resulted in an insignificant amount of germination of impermeable rose clover seed.

High Temperature Treatment of Impermeable Rose Clover Seed

In consequence of the partial breakdown of rose clover seed impermeability as a result of allowing ripe seed to lie on the soil surface during the summer heat, and the negative results of cool season experiments, high temperature treatments were applied to samples of the rose clover seed collected in 1958. Since temperatures of about 140°F (60°C) were measured in rose clover calyces on the soil surface, this temperature was applied for 2 hr in a forced draft electric oven to impermeable seed from the University Farm in a preliminary test. The impermeable seed content was reduced from the original 100% to 65% with a corresponding increase in germination.

Subsequently, seed of rose clover was tested similarly by heating for one hr at a series of temperatures from 100-220°F (37.8-104.4°C). Lots of 50 seeds were used from the seed obtained in the 7 monthly collections at each of 7 locations in single replication. The data for the 7 locations were averaged for presentation in Table IV.

Seed treated with temperatures from 100-150°F maintained a percentage of impermeable seed of 96% or more, averaged over the collection dates. The June collections dropped below 90% impermeable seed when treated with 160°F, the July, August, September, November and December samples dropped below 90% when treated at 180°F, and October when treated at 190°F. The decline of impermeability with increasing temperature was sharpest in the June seed collection, and sharper for July and August than for the later collections. At 220°F, the highest temperature used, 17-33% of the seed remained impermeable.

The difference between 100% and the percentage of impermeable seed is made up of 2 components, the germination and dead seed percentages. Germination largely accounts for the difference up to 180°F for June and 200°F for the later collections. The June collections exceeded 10% germination at 160°F, and the July, August, September and December collections exceeded 10% germination at 180°F. The October collections exceeded 10% germination at 190°F and September collections at 200°F. The maximum germination percentage occurred at 200°F for the August collections, although this seems to have little ecological significance. On the average the germination percentage droped sharply when temperature levels reached 30 to 40° above the level at which seed coat impermeability began to break down. Beyond these temperatures heat destroyed the viability of a large percentage of the embryos as indicated by the dead seed data in Table IV.

At the time the temperature treatments were performed, the moisture content of the seed ranged from 1.8-6.6%. The moisture in seed collected

TABLE IV. Effect of time of collection on high temperature response of impermeable rose clover seed, one hour treatment. Data are means for 7 locations

TEMPERATURE		IMPERMEABLE %							GERMINATION %							DEAD %						
°F	°C	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Untreated		94	98	95	95	95	98	99	6	1	5	4	5	2	0	0	1	0	1	0	0	1
100	37.8	93	99	95	95	95	98	98	6	1	4	5	5	1	1	1	0	1	0	0	1	1
110	43.3	94	97	97	93	96	97	98	6	1	2	6	3	2	1	0	2	1	1	1	1	1
120	48.9	97	95	99	95	97	96	98	3	4	1	4	3	3	2	0	1	0	1	0	1	0
130	54.4	94	97	97	95	93	99	99	5	2	1	3	6	1	1	1	1	2	2	1	0	0
140	60.0	93	96	96	94	99	99	98	6	3	2	5	1	1	1	1	1	2	1	0	0	1
150	65.6	90	96	97	93	97	98	98	8	3	1	5	2	1	2	2	1	2	2	1	1	0
160	71.1	89	96	97	93	95	98	98	11	3	3	5	5	1	2	0	1	0	2	0	1	0
170	76.7	80	97	93	94	96	97	96	13	2	4	3	4	2	3	7	1	3	3	0	1	1
180	82.2	45	66	61	79	90	89	86	21	30	30	15	7	9	11	34	4	9	6	3	2	3
190	87.8	26	57	52	78	87	82	84	19	36	35	16	9	16	13	55	7	13	6	4	2	3
200	93.3	21	42	33	57	69	67	62	18	42	50	30	20	28	28	61	16	17	13	11	5	10
210	98.9	19	25	29	27	36	34	30	0	0	0	26	40	20	32	81	75	71	47	24	46	38
220	104.4	17	29	26	26	33	33	28	0	0	0	10	17	8	6	83	71	74	64	50	59	66

in June ranged from 3.8-6.6%, in July 2.8-5.1%, in August 2.9-5.1%, in September 1.8-4.9%, in October 2.8-4.2%, in November 2.4-3.5% and in December 2.2-3.1%. These moisture percentages may be compared with the average moisture content of 2.4% for rose clover tested directly from the field in midsummer. Seed collected in June had the highest average moisture content and showed the greatest variability in temperature response among locations. The germination percentages of the Napa and Solano collections in June were increased by a temperature treatment lower than the remaining collections.

Ecological Significance of Seed Coat Impermeability

The soil-atmosphere interface is a harsh environment because of the rapid fluctuations between extremes of temperature and moisture. The most vulnerable period in the life cycle of an annual legume, germination and early seedling growth, is spent in the proximity of this interface. Species persistence can be materially affected by the degree to which it has the adaptive physiological characteristic of seed coat impermeability. An ample supply of impermeable seed which becomes progressively permeable over a long period of years minimizes the risk of unfavorable temperature and moisture conditions in any one germination and establishment interval, and increases the probability of persistence.

Crimson clover.—In California range plantings crimson clover does not persist more than 2 or 3 yr after planting except on sites having an unusually favorable moisture regime. After maturity there is a rapid decline in impermeable seed content of presently used varieties of this species (Fig. 3). By the advent of the first effective autumn rain, usually in November, the impermeable seed percentage of crimson clover has declined to a very low value. Hence, the lack of persistence appears to be closely associated with the low level of impermeable seed and consequent susceptibility of seedling destruction by drought following initially favorable germination conditions.

The development and use of strains with an inherited ability to maintain a satisfactory amount of impermeable seed over a more extended time would be likely to increase the persistence of this

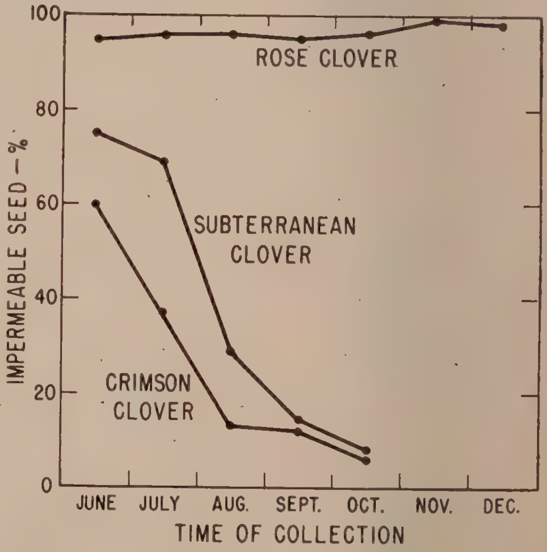

FIG. 3. Impermeable seed percentages of crimson, subterranean and rose clovers, averages of data from all collection sites.

valuable forage plant. The development of a crimson clover strain with a high content of impermeable seed was recently reported by Bennett (1959).

Subterranean clover.—Where well established initially, subterranean clover persists for many years, approaching the long term persistence of rose clover under California conditions. Subterranean clover persists particularly well under continuous close grazing. The fact that a small percentage of impermeable seed is present by the time of the first autumn rains seems to be of less importance with this species than with crimson clover. The persistence of subterranean clover under grazing is controlled more by its growth form, particularly its prostrate branching habit than by seed characteristics. Most important is the fact that as its many axillary inflorescences mature, the supporting peduncles bend towards the ground, and many seed-containing burs bury themselves just below the soil surface. The mechanism is effective in making much seed unavailable to foraging animals. Hence, large seed crops are self-planted with a minimum of consumption by domestic livestock and other fauna, and the meager impermeable seed supply is conserved.

A post-harvest dormancy in which imbibed seeds remain ungerminated has been studied in subterranean clover (Ballard 1958 and Morley 1958). Low temperature, exposure to 0.5-5.0% carbon dioxide atmosphere, exposure to moist soil, coating the seed with absorbent materials such as activated carbons, and removal of testa accelerate release from this dormancy. However, since the dormancy is relatively transitory being important only in the year following seed setting Morley (1958) concluded that long term conservation in subterranean clover is more dependent on production of impermeable seed. Post-harvest dormancy was expressed in less than 2% of the seed collected for the experiments reported here.

Rose clover.—The rose clover strain developed by Love and Sumner (1952) and used in the plantings sampled in this study produces an extremely high percentage of impermeable seed. This has posed no problem in initial establishment using commercially produced seed because the threshing process scarifies enough seed to permit a satisfactory level of germination. Commercial seed lots also contain enough impermeable seed to permit a "second chance" if the quick germinating individuals subsequently succumb to an unfavorable environmental condition (Williams et al. 1957). However, in volunteer stands the break down of seed coat impermeability in a significant portion of the seed produced by this annual species is of importance to continuance of a desirably dense plant population, particularly in the early years after establishment. This aspect of the problem was one of the primary concerns of this study.

The mild winter environment at the University Farm either immediately below or above the soil surface was not conducive to break down of impermeability. However, both field and laboratory results suggest that high temperatures of the summer microclimate, especially at the soil surface, induce a significant amount of permeability. Late summer break down of impermeability would appear to be a more useful mechanism to population continuance than winter break down since early germination provides the developing plant with a full growing season. In comparison a winter-induced germination would result in a much abbreviated growing season and much more intense competition from rapid growing resident annuals, which would have begun their growth cycle with the first effective autumn rains. The consequence of winter break down of impermeability in a Mediterranean-type climate would be a much reduced ability to produce forage and seed.

A point which this series of experiments does not resolve is whether a net accumulation of heat units causes break down of impermeability or whether there is some intrinsic effect of fluctuating temperatures per se. Although fluctuating temperatures have been shown to be effective in reducing impermeability of subterranean clover seed (Aitken 1939) no definitive tests of these hypotheses have been reported for high temperatures.

The outstanding ability of rose clover to persist under grazing and adverse soil and climatic conditions may be concluded to be due in large measure to its prolific production of impermeable seed.

SUMMARY

Ecological aspects of seed coat impermeability were studied in 3 species of annual legumes: crimson, subterranean and rose clovers (*Trifolium incarnatum, T. subterraneum* and *T. hirtum*). The pattern of impermeability was explored relative to time after seed maturity in locations under the influence of the Mediterranean-type climate of California. The impermeable seed percentage for crimson clover declined to a low level during the summer months after seed maturation at all locations sampled. Subterranean clover followed a similar though slightly delayed pattern of decline with the exception of one site under a marine

influence which maintained a moderate amount of impermeable seed into the autumn period. Rose clover maintained a very high percentage of impermeable seed throughout the summer, autumn and winter months at all locations sampled.

In further studies with rose clover it was shown experimentally that a mild winter environment was not conducive to the break down of seed coat impermeability of seed placed either immediately above or below the soil surface. It is inferred from field results that the high temperatures of the summer-imposed microclimate, especially at the soil surface, induced a significant amount of permeability. Laboratory tests with elevated temperatures lend support to this thesis. In the light of the ecological significance of seed coat impermeability, it is postulated that summer break down of impermeability has a survival advantage to a winter annual species over winter break down of impermeability. The observed persistence of rose clover under adverse conditions is largely due to its prolific production of impermeable seed.

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THE FOREST VEGETATION OF THE APOSTLE ISLANDS, WISCONSIN[1]

E. W. Beals and Grant Cottam[2]

The Apostle Islands, located at the tip of the Bayfield Peninsula in Lake Superior, are the northernmost land areas in Wisconsin (Fig. 1). Because of their location and their isolation from each other and from the mainland, they have developed as a ready-made experiment for the ecologist. The islands have reasonably uniform topography and geology, but they have had different histories of fire, logging, browsing, and agriculture, thereby providing an excellent opportunity for assessing the effects of these historical factors. In addition, some of the islands have virgin forests, and most of the islands have vegetation that has been undisturbed by man for at least half a century. This project was initiated because of the excellent opportunity provided by the islands for assessing the effect of deer on vegetation, and in the course of this investigation a thorough study of the vegetation was made. This paper is concerned primarily with the vegetation of the islands, the results of the deer study having been reported elsewhere (Beals *et al.* 1960).

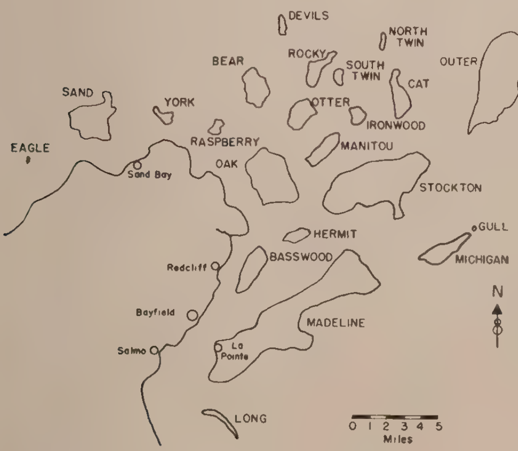

Fig. 1. A map of the Apostle Islands.

Literature Review

Kittredge (1938) studied the aspen communities of northern Wisconsin and Minnesota and differentiated stands on the basis of the vegetation associated with the aspens. He was interested partly in using plant indicators for site index. Thomson (1945) analyzed the total vegetation of the Brule River region. His work was primarily descriptive.

The first quantitative sociologic study in northern Wisconsin of the hemlock-pine-hardwoods forest type was done by Potzger (1946), whose interest lay primarily in the historical record. He presented evidence that climax in this region is not pine, as suggested by some workers, but hemlock-hardwoods. Stearns (1949, 1951) studied the present composition and the historical record of stands of the sugar maple-hemlock-yellow birch type. He found that there is a tendency for sugar maple to increase in importance as a stand ages.

Brown and Curtis (1952) studied the upland conifer-hardwoods of northern Wisconsin, ordering their stands along a gradient by the relative importance of trees, from jack pine at one end to sugar maple and beech at the other. The position of a stand along this gradient indicated its relation to xeric or mesic stages. Christensen, *et al.* (1959) surveyed the lowland vegetation in northern Wisconsin and formulated a similar gradient. One end had tamarack as most important, and the other end was dominated by sugar maple and beech. Maycock (1957) discussed the southern fringe of the boreal forest in the Lake States region, including many stands in Wisconsin. He ordered his stands both on a moisture gradient and on a multidimensional ordination based on a large group of component species, and found results of both methods similar.

Description of the Region

The climate of the Apostle Islands is somewhat tempered by the surrounding water, but winters are still severe. January mean temperature is 12° F in Bayfield County. Summers are cool and damp, with a mean July temperature of only 65°. Growing season is somewhat longer than in nearby inland areas, extending from about the end of May to the end of September. Annual precipitation averages 27 in., with July the wettest month. There is an average of 80 in. of snowfall per year, and snow cover lasts through most of the winter (U.S.D.A. 1941).

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[1] This study was conducted in cooperation with the Wisconsin Conservation Department and was financed with Federal Aid to Wildlife Restoration funds under Pittman-Robertson Project Number W-79-R.

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The islands are composed of drift hills of red sandy clay resting on red sandstone, and were once part of the mainland in postglacial times (Van Hise and Leith 1911). There are 22 islands in the group, ranging in size from a few acres to over 13,000 acres. Most of the islands are low and flat, with an average elevation of less than 100 ft above lake level. Two islands, Oak and Basswood, are higher, Oak Island having an elevation of about 480 ft above lake level, and Basswood about 150 ft.

Madeline Island, the largest of the Apostles, was a center of activity for Indians prior to the arrival of white man, and for French explorers, missionaries, and traders during the 17th and 18th centuries. A small French settlement called La Pointe developed in the 1690's on Madeline, where Indians were less apt to attack the white men. This community, somewhat moved from its original location on the island, still exists today. As the fur trade declined and the lumber industry boomed during the nineteenth century, other white men moved into the region. Quarries were opened on several islands.

Except for Madeline, none of the islands support year-round human populations. Madeline has a system of roads, supports a few farms and has a small tourist trade. Sand, South Twin, Basswood, Rocky, and Stockton all have a few summer cabins or fishing camps, and a few others have deserted evidences of human habitation though this has not been a serious factor in the development of the vegetation of the islands.

Logging has had an important influence on the vegetation. Most of the islands have suffered repeated cuttings over the past two centuries. Within the last 20 yr much of Oak Island has been selectively cut for *Quercus borealis* and practically all merchantable trees have been cut from Otter and Ironwood Islands. At the present time Outer Island is being logged, but several undisturbed stands remained at the time the field work for the present study was conducted. Virgin stands exist on several of the islands, many of which are on land owned by the federal government.

Fire is another important factor. A number of fires have occurred on Madeline, and Stockton and Oak have both had extensive fires in the past 10 yr.

The white-tailed deer is perhaps the most important animal influence on the vegetation. Some islands, such as Basswood, Hermit, Madeline, and possibly Oak have had long established deer herds. Others such as Stockton, Rocky and South Twin have been invaded by deer rather recently. Outer, North Twin, Devils, York, and Sand have never had permanent populations, as far as is known. Populations vary from light density on Cat and Michigan to moderate on Bear, Manitou, and Otter, to heavy on Rocky, Hermit, Basswood, South Twin, Stockton, Oak and Madeline Islands.

FIELD METHODS

Seventy-five stands located on 18 of the 22 islands were studied. The remaining 4 islands were either too small or too recently disturbed to possess stands of adequate size. The stands were selected to give a representative sample of the forests of the region, with emphasis on the less disturbed vegetation. All were free from recent human disturbance. Criteria for the selection of stands were adequate size (10 acres or more), uniform topography, and absence of major disturbance except for browsing. Homogeneity was determined after the stand had been sampled. The sample was divided into 4 equal subsamples representing 4 approximately equal areas of the stand and the observed number of trees of the dominant species in each subsample was compared with the expected number. A chi-square test of homogeneity was then applied (Snedecor 1956). Three of the stands used were non-homogeneous at the .05 level, but this number would be expected to exceed the .05 level in a sample of this size and all stands were used in the analysis.

The trees and saplings were sampled by the quarter method described by Cottam and Curtis (1956). Forty points were used in each stand, except in a few cases. The points were located by pacing a given distance (depending on the size of the area) along a compass line. The distances from the point to the nearest tree (over 4 in. dbh), and the nearest sapling (1 to 4 in. dbh) in each quarter were measured. Basal areas of the trees were recorded. At alternate points, the herbs, shrubs, and tree seedlings (under 1 in. dbh) within a 1 sq m quadrat were listed. For most stands this amounted to a 20-quadrat sample.

The taxonomic nomenclature follows Gleason (1952).

STATISTICAL METHODS

The following analytic characters were calculated for each stand: the absolute and relative frequencies of each species of herb, shrub, and tree seedling; the absolute and relative frequency, absolute and relative density, and absolute and relative dominance of each species of tree; the importance value (sum of relative frequency, relative density, and relative dominance) for each species of tree; relative density and absolute frequency of sapling species; and the total trees per acre, total dominance per acre, and the total saplings per acre.

The stands were arranged in a three-dimensional ordination according to the method of Bray and Curtis (1957), with a modification described by Beals (1960). The ordination is based on the coefficient of community, $\frac{2w}{a+b}$, where a is the sum total of quantitative values for one stand, b is the sum total for the other stand, and w is the sum of the lower values for each species common to both stands. All species of trees were included in the calculations of the coefficient, and all species of herbs and shrubs occurring in 5 or more of the 75 stands. Two quantitative values for trees were used—absolute density and absolute dominance. Only one value, absolute frequency, was used for shrubs and herbs. This gave the tree species twice the weight of the herb species in determining the coefficients of community. Twenty-one tree species and 53 herb and shrub species were used in calculating the coefficients of community. Since two values for each tree species were used, the total number of possible tests for each stand was 95.

RESULTS

The data on the tree species are summarized in Tables I and II. Table I is a list of all tree species encountered in the study. The presence values show the number of stands out of the total of 75 in which each species occurred. The second column of the table is the arithmetic mean of the importance value (sum of relative frequency, relative density, and relative dominance) for the species in those stands in which the species occurred. A high presence coupled with a high importance value indicates that the species occurs in most of the stands and is an important constituent in those stands in which it occurs. Three species are clearly the most widespread and important: *Betula lutea, Thuja occidentalis,* and *Betula papyrifera.* One or another of these species is the leading dominant in almost two-thirds of the stands. *Abies balsamea* is also present in most of the stands, but usually in much lower numbers. It is the leading dominant in only 3 stands, but is the second dominant in 16. *Sorbus americana* is of special interest in this region. This tree is present, though usually in fairly small numbers, in almost two-thirds of the stands and is the second dominant in one stand. In most of Wisconsin *Sorbus* usually does not attain tree size, but on the Apostle Islands there are trees as large as 2 ft dbh.

TABLE I. A summary of tree data for 75 stands.

Species	Presence No. stands	Ave. I. V.*	No. stands 1st dom.	No. stands 2nd dom.
Abies balsamea	66	39.4	3	16
Betula lutea	66	62.8	19	17
Acer rubrum	63	18.7	0	3
Betula papyrifera	63	52.1	12	11
Thuja occidentalis	58	62.3	18	10
Acer saccharum	56	41.1	7	4
Sorbus americana	46	9.8	0	1
Tsuga canadensis	41	31.9	4	4
Quercus borealis	27	23.3	2	2
Populus tremuloides	22	52.4	4	1
Prunus pensylvanica	21	6.8	0	0
Ostrya virginiana	14	5.8	0	0
Pinus strobus	14	40.7	2	2
Tilia americana	11	11.8	0	2
Populus grandidentata	8	27.0	1	0
Picea glauca	7	18.5	0	0
Pinus resinosa	5	99.1	2	1
Fraxinus nigra	3	2.2	0	0
Pinus banksiana	3	68.3	1	0
Picea mariana	2	65.0	0	1
Fraxinus americana	1	1.9	0	0
Larix laricina	1	13.6	0	0

* Average importance values in those stands where present.

TABLE II. The number of stands with each combination of first two dominant tree species

	Betula papyrifera	Pinus strobus	Thuja occidentalis	Betula lutea	Tsuga canadensis	Acer saccharum	Tilia americana	Quercus borealis	Acer rubrum	Sorbus americana	Pinus resinosa	Picea glauca	Populus tremuloides	Pinus banksiana	Picea mariana
Acer saccharum							2	1							
Tsuga canadensis									1						
Betula lutea					7	7				1					
Thuja occidentalis				12		1									
Pinus strobus			1								3				
Betula papyrifera				7	4			3	1			1	4		
Abies balsamea	3			7	5				1				1	1	1

Table II shows the various species combinations of first and second dominants. The most frequent combination is *Betula lutea* and *Thuja occidentalis,* which occurs in 12 of the 75 stands. The species occurring in combination with the most other species is *Abies balsamea.* This tree, although rarely the leading dominant in a stand, seems to possess the ability to grow in almost any habitat in this region, and occurs as either the first or second dominant with species as widely divergent in their habitat requirements as *Pinus banksiana* and *Picea mariana.* It is of interest that in this fairly small area with a relatively uniform environment, 16 different species occur as either the first or second dominant, and 23 different combinations of species occur as the first and second dominants in the 75 stands.

Table III lists 59 species of shrubs and herbs occurring in the stands. The table includes all species that occurred in 5 or more stands and all species that occurred in any stand with a frequency of 50% or more. This list includes about 40% of the shrub and herb species found. The listing is in order of decreasing presence, with the shrubs and herbs listed separately. The last column gives abbreviations of the dominant tree species in the stands in which the shrub and herb species attained their greatest frequencies.

Among the shrubs, *Acer spicatum* and *Taxus canadensis* were the most nearly ubiquitous, occurring in more than two-thirds of the stands, and having frequency percentages of more than 50 in almost half the stands. None of the remaining shrubs commonly occurred with frequencies of more than 50%, although *Corylus cornuta* did occur in over half the stands.

In comparison with the shrubs, the herbaceous species show a greater number of species with relatively wide occurrences. Sixteen species occurred in more than one-third of the stands. Ten of the herbaceous species listed reached their highest frequencies in stands dominated by sugar maple, in spite of the fact that only 7 stands had sugar maple as the dominant species. This indicates that stands dominated by sugar maple present a habitat situation that is quite different from that of the other forests.

The ordination of stands was computed for 3 different axes on the basis of stand similarities, but since it is not possible to present a 3 dimensional figure of this complexity on paper, only the first two axes are shown in the figures. Results for the third axis are presented in the discussion. Perhaps the most striking feature of the ordination is the grouping of many stands within a rather restricted area of the figures. This area corresponds to the area of overlap of the regions on the ordination where yellow birch and white cedar attain importance values of 75 or greater as shown in Figure 2. The data in Table I show that half the stands have one or the other of these species as the leading dominant, and 12 stands have these two species occurring together as first and second dominants. Another interesting aspect of the ordination is the remarkably clear separation of the regions where the most common tree species reach importance values of 75 or more.

DISCUSSION

In spite of their fairly uniform topography, the Apostle Islands offer a variety of habitats. The low islands, those with a maximum elevation above lake level of less than 100 ft, are usually flat, with steep slopes connecting the upland region to the rocky beaches. On the windward sides there is often no beach at all, only precipitous sandstone cliffs. On the leeward sides, there is on some islands a well developed sand bar that may be several hundred feet long. The uplands are poorly drained and resemble the lowland areas of the adjacent mainland. Two islands, Devils and Stockton, have well developed bogs. Some sand bars support stands of pine trees; others have no trees at all. It is only on the well drained slopes of the two higher islands, Oak and Basswood, that stands similar to those of the upland areas of the mainland occur.

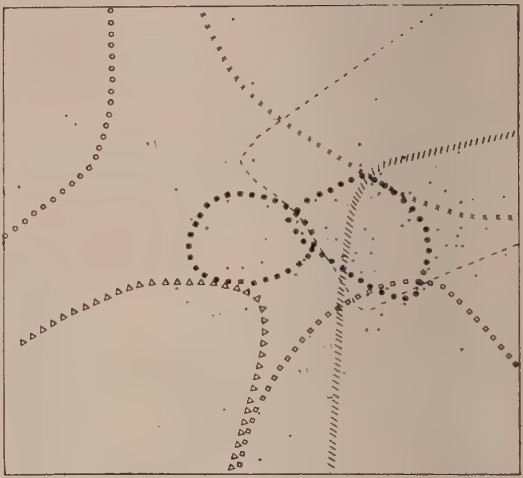

FIG. 2. Patterns of 8 tree species on the ordination. Contour lines surround those stands which have an importance value greater than 75 for each tree species. Open circles—*Pinus resinosa;* open triangles—*Quercus borealis;* open squares—*Acer saccharum;* diagonal lines—*Betula lutea;* dotted line—*Thuja occidentalis;* X's—*Abies balsamea;* closed circles—*Tsuga canadensis;* closed squares—*Populus tremuloides.* Small dots represent stand location on the ordination.

In sampling the forests of these islands, an attempt was made to select stands representing all of the forest types that occurred. Consequently, it is probable that the more common types were under sampled, and the relatively rare types are represented in the data in a much greater proportion than their actual areal extent would justify. On an areal basis most forests were on the poorly drained soils of the lowlands. These areas were normally dominated by stands having *Thuja occidentalis* and *Betula lutea* as dominant species. Other tree species in these stands were *Abies balsamea, Betula papyrifera, Tsuga canadensis,* and *Acer saccharum*. The understory was dominated by two shrubs, *Acer spicatum* and *Taxus canadensis*, the former more common in slightly drier sites than the latter. *Taxus* gives these stands an aspect entirely unlike that of any forests on the Wisconsin mainland. On some of the islands it is so dense as to be almost impenetrable. In the more open areas it attains a height of more than 8 ft. This species is apparently very sensitive to browsing by deer (Beals *et al.* 1960), and its frequency is closely correlated with the size of the deer populations.

The most common herbs in these stands are *Clintonia borealis, Dryopteris austriaca, Lycopodium lucidulum, L. obscurum, Maianthemum canadense,* and *Trientalis borealis*. These stands resemble those of the level, wet-mesic lowlands along parts of the south shore of Lake Superior, except for the greater importance of *Taxus* on the islands. There is often standing water in the forests, and the water-holding capacity of the soil usually is 300% or more. The soil is moderately acid (pH about 5.0), commonly a sandy clay, with a litter layer usually of less than one inch.

In regions that have never been logged, on Outer, North Twin, and Devils Islands, the stands on similar sites are somewhat different. *Betula lutea* is still a dominant species, but *Thuja occidentalis* is largely replaced by *Tsuga canadensis*. These are the most magnificent forests on the islands, with individuals of the two dominant species often attaining sizes of 1000 sq in. or more basal area. One *Betula lutea* tree on North Twin Island had a basal area in excess of 1500 sq in. The herb and shrub species are not appreciably different from those of the *Thuja—Betula lutea* forests.

Pine forests are typically located on sand bars on the lee shores of some of the islands. On the ordination in Figure 2, they are located on the upper left margin. Three such stands were studied. They had *Pinus resinosa* as the dominant tree, with *Pinus strobus* the second dominant. *Pinus banksiana* and *Betula papyrifera* were present in small numbers. Ericaceous species dominated the understory, with *Arctostaphylos uva-ursi, Vaccinum myrtilloides, V. angustifolium, Gaylussacia baccata* and *Epigaea repens* common in one or more stands. Other species included *Maianthemum canadense, Cornus canadensis, Pteridium aquilinum,* and *Trientalis borealis*. Two other stands with a high importance of *Pinus* spp. were studied. They were on heavier soil and occurred with *Thuja occidentalis, Abies balsamea, Picea glauca, Populus tremuloides,* and *Betula papyrifera*. *Maianthemum canadense, Linnaea borealis, Cornus canadensis,* and *Galium triflorum* were common in the understory.

Pinus strobus also occurred as isolated individuals throughout many other stands on the islands. The fact that *P. strobus* is a valuable lumber tree has led to its selective removal from the islands where lumbering has occurred, but these isolated trees still remain in the less disturbed stands.

The mesic forests, somewhat drier than the *Thuja-Betula lutea* forests are confined to the relatively rare well-drained habitats. Here, *Quercus borealis* reaches its optimum development. Unfortunately logging has removed much of the original forest. One fairly young red oak stand had a 50% relative density of the dominant tree, with *Acer rubrum* and *Acer saccharum* as important species and *Abies balsamea, Betula papyrifera, Tsuga canadensis* and two *Populus* spp. present in small amounts. The more mature forests (red oak-sugar maple) were selectively cut for red oak about 20 yr ago. The maples consequently occurred in almost pure stands, but these stands were more open than the maple stands of the adjacent mainland. On the north slopes, these open stands had an understory of *Acer saccharum* saplings and seedlings, but on the south slopes *Corylus cornuta* and *Acer spicatum* were more common.

Aspen stands are characteristic of areas of more recent disturbance. They are especially common on Madeline, Oak, Outer and Stockton Islands. In most cases the second dominant is *Betula papyrifera*, and the understory contains *Fragaria virginiana, Aster macrophyllus, Pteridium aquilinum,* and *Cornus canadensis*.

The relationships between these various stand types can be seen in the ordination in Figure 2. The dots on the figure represent the locations of the stands. The majority of stands are grouped around the area of overlap of *Betula lutea* and *Thuja occidentalis*. This could, of course, be due to a subjective selection of this particular type of stand, but the reverse is more nearly the case. An attempt was made to sample the most typical habitats on all the islands, but any divergent forest types were also sampled to obtain data on the complete range of forest vegetation. Consequently, the distribution of dots on Figure 2 actually gives greater weight to the vegetation types different from this typical *Betula lutea—Thuja* forest than their importance on an areal basis would justify. The aspen stands are also under-represented.

Since this ordination is based solely on vegetational criteria, no linear correlations with environmental factors can be expected. However, several trends are indicated. A moisture gradient starts with the relatively dry pine stands at the upper left edge of the figure and moves in a circular fashion counter-clockwise through the *Quercus borealis, Acer saccharum, Betula lutea, Thuja occidentalis*, and *Abies balsamea* stands. The wettest stand, a *Picea mariana* swamp, is at the top center of the figure.

A light gradient apparently runs from the upper left to the lower right corners. An attempt was made to measure light intensity in these stands, but due to the exceedingly cloudy weather during the years in which the stands were sampled, the data are too fragmentary to be meaningful. However, data from other sources (Curtis 1959) indicate that of the forest types present on the Apostle Islands the pine and conifer swamp stands normally have the highest light intensities, and the sugar maple stands the lowest.

The upper left to lower right trend is also the general direction of two separate patterns. The upland hardwood continuum of Brown and Curtis (1952) moves from pines through red oak to hemlock and sugar maple, a counter clockwise circular course on Figure 2. The lowland continuum for the same region (Christensen *et al.* 1959) follows a clockwise course on Figure 2 from black spruce through white cedar, hemlock, and yellow birch, to sugar maple.

The center of the ordination is occupied by the two species of *Populus, Betula papyrifera,* and *Tsuga canadensis*. In the two-dimensional ordination, *Populus* and *Tsuga* overlap, but on the third dimension of the ordination they are widely separated. *Betula papyrifera* is rather widely scattered through the center of the ordination on all 3 axes and, as indicated in Table II, is co-dominant with many other species. The third axis is apparently related to disturbance.

The ordination pictured in Figure 2 bears a strong resemblance to the ordination of the northern upland forest of Curtis (1959, Fig. 31). Especially striking are the similar locations of *Pinus* spp., *Quercus borealis; Tsuga canadensis,* and *Acer saccharum.* Differences between the two ordinations are possibly due to the inclusion in the present ordination of stands listed by Curtis as wet mesic or wet, and consequently not considered by him in his ordination of the upland stands. The two ordinations were constructed by the same methods, but none of the data from the present study were used by Curtis. This suggests that the relationships of the species as depicted by the ordination are really characteristics of the vegetation and not due to the fortuitous manipulation of the data. The number of stands involved in the ordination is so great that the number of possible arrangements of these stands on a two-dimensional ordination is almost infinite. That groups of workers using different sets of data arrive at such similar arrangements is strong corroboration of the validity of the method.

The shrub and herb species are plotted in Figures 3, 4, and 5 on the same two axes of the ordination. Three species, *Vaccinium myrtilloides, Maianthemum canadense,* and *Cornus canadensis* are found with their greatest frequencies in both the dry pine stands and the wet *Abies balsamea-Betula papyrifera stands.* That these species are not responding to a moisture gradient is obvious. The factors in common in these two communities are fairly high light, acidity of the soil (pH 4.8 in the pines and 4.2 in the wet stands), and low water availability—either actual or "physiological dryness."

Taxus canadensis occurs with its highest frequency values in regions where *Thuja occidentalis* and *Betula lutea* are the dominant tree species, but is absent from stands containing these two tree species that are near the center of the ordination. This is probably due to the extreme sensitivity of *Taxus* to disturbance. The effect of deer on *Taxus* has already been mentioned. Apparently

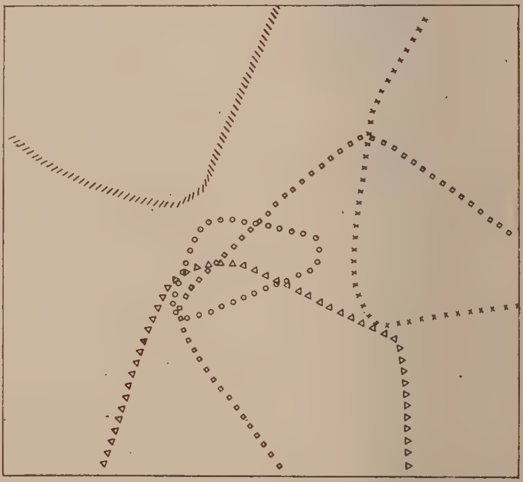

FIG. 3. Patterns of 5 shrubs on the ordination. Contour lines surround those stands which have frequency greater than one-half the maximum frequency of each shrub species. Diagonal line—*Vaccinium myrtilloides;* circles—*Rubus hispidus;* triangles—*Corylus cornuta;* squares—*Acer spicatum;* X's—*Taxus canadensis.*

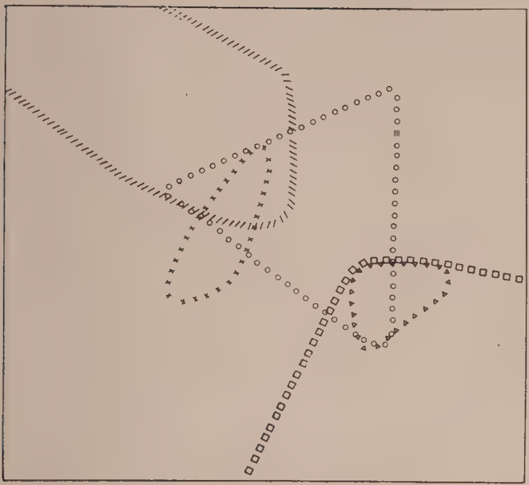

FIG. 4. Patterns of five widely distributed herbs. Contour lines surround those stands which have a frequency greater than one-half the maximum frequency for that species. Diagonal lines— *Maianthemum canadense;* X's —*Trientalis borealis;* circles— *Clintonia borealis;* triangles—*Lycopodium obscurum;* squares—*Dryopteris austriaca.*

Taxus responds similarly to other types of disturbance as well.

The 5 species plotted in Figure 4 are the herbs that are most nearly ubiquitous on the Apostle Islands. Their presence values are given in Table III. In spite of the fact that they all occur in 80% or more of the stands, the areas in which they reach their optimum development are fairly restricted. This is especially true of *Dryopteris austriaca.* The stands in which it reaches its maximum frequencies do not have the same dominant tree species, but are located very close to each other on the ordination. If plant communities on these islands were defined in terms of most important tree species, *Dryopteris* would do well in many communities. Actually it reaches its maximum development in a highly restricted area that does not coincide with the area of maximum importance of any single tree species.

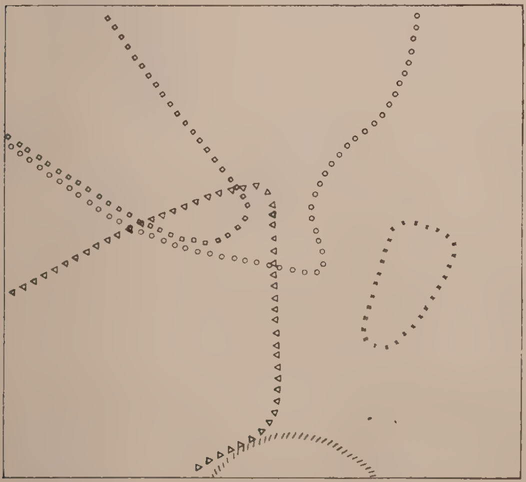

FIG. 5. Patterns of 5 other herbs. Contour lines surround those stands which have a frequency greater than one-half the maximum frequency for that species. Squares —*Pteridium aquilinium;* circles—*Cornus canadensis;* triangles—*Aster macrophyllus;* diagonal lines—*Streptopus roseus;* X's—*Lycopodium lucidulum.*

Very few herbaceous species reach their maximum frequencies in the *Thuja-Betula lutea* stands. Of the herbs listed in Table III, only *Thelypteris phegopteris* shows preference for this type of stand. It is fairly uncommon on the Apostle Islands with a maximum frequency in any stand of only 25%. A possible explanation for this lack of herbaceous species with a preference for the type of stand most common on these islands is the very high density of two shrubs, *Taxis canadensis* and *Acer spicatum.* These two shrub species may occur with very high density, and the resulting low light intensities on the forest floor may be responsible for the fact that no herb species do well there.

CONCLUSIONS

The forests of the Apostle Islands are fairly representative of the forests of the remainder of northern Wisconsin. There are, however, some important differences. First of these is the relative scarcity of well-drained habitats. One island, Oak, has most of the stands that can be considered characteristic of the normal upland habitats of the mainland. The other islands are mostly low and flat, with poor subsurface drainage, and have vegetation similar to that of lowland sites on the mainland. The most common forest type is a *Betula lutea-Thuja occidentalis* forest with *Abies balsamea* and *Betula papyrifera* as common additional species. *Sorbus americana,* while not very common, is much more important in these stands than it is elsewhere in Wisconsin.

The coniferous shrub, *Taxus canadensis,* is the most common understory shrub. Its high densities on islands without deer and its rapid disappearance on islands where deer have been recently introduced leads to the conclusion that it was probably a more important component of the vegetation of much of northern Wisconsin prior to the large increase in the deer population that accompanied lumbering and protective deer legislation.

The ordination of stands shows that discrete communities do not exist and, had stands been

TABLE III. A summary of shrub and herb data for 75 stands

Species	Presence No. stands	Max. Freq.	No. stands Freq.≥50%	Dominant Canopy Trees
a) shrubs				
Acer spicatum	58	95%	37	As Bl
Taxus canadensis	55	100	35	Bl Bp To
Corylus cornuta	44	40	—	As Qb
Rubus hispidus	25	35	—	Bp Pt Bl
Diervilla lonicera	21	65	2	Bp Pt
Lonicera canadensis	20	20	—	Bp Qb
Rubus parviflorus	19	40	—	As Bp Qb
Amelanchier sp.	17	40	—	Ps To
Rubus strigosus	11	15	—	Pt
Vaccinium angustifolium	8	75	2	Pr Ps
Vaccinium myrtilloides	7	60	2	Pr Ps Ab
Alnus rugosa	6	20	—	Ab To
Ribes americanum	6	10	—	Bl Sa
Rubus pubescens	5	25	—	Bl Ps Tc
Gaylussacia baccata	2	50	1	Pr Ps
b) herbs				
Trientalis borealis	72	95	7	Ab Bp
Clintonia borealis	63	85	12	Bp Bl
Dryopteris austriaca	62	75	11	Bl Tc To
Maianthemum canadense	62	100	10	Pb Pr Ps Pt
Lycopodium obscurum	59	55	1	As
Viola spp. (stemless)*	56	85	6	Bp Pt To
Cornus canadensis	47	65	3	Ab Bp
Aralia nudicaulis	45	85	6	Bp Pt
Streptopus roseus	45	85	2	As Bl
Lycopodium lucidulum	44	80	7	As Bl Tc
Lycopodium annotinum	42	30	—	Ab To
Carex spp.**	41	75	3	Ab To
Galium triflorum	38	85	2	Bp Pt
Gymnocarpium dryopteris	31	25	—	As Bl To
Aster macrophyllus	29	100	8	Bp Pt
Thelypteris phegopteris	25	25	—	Bl To
Lycopodium clavatum	17	10	—	Bp Pt
Impatiens biflora	16	15	—	Bl Ps Pt
Coptis trifolia	15	50	1	As Ps
Fragaria virginiana	14	100	1	Pt
Melampyrum lineare	14	60	3	Bl Pr Ps
Gaultheria procumbens	13	100	3	Bp Qb
Corallorhiza maculata	12	5	—	Ab Pt Qb
Pteridium aquilinum	12	100	2	Pr Pt
Linnaea borealis	11	65	1	Ps To
Osmorhiza claytoni	10	20	—	Ps To
Petasites frigidus	10	25	—	Ps Pt
Osmunda cinnamonea	9	5	—	Bl Bp To
Oxalis acetosella	8	10	—	Bl Tc To
Streptopus amplexifolius	8	15	—	As Bl
Cystopteris fragilis	7	25	—	As Bl
Lycopodium complanatum	7	15	—	Ab Bp
Mitchella repens	7	15	—	As Bl
Aster sagittifolia	6	25	—	Bp Pt
Circaea alpina	6	10	—	Bp Pt
Equisetum arvense	6	35	—	Ab Pt
Lactuca canadensis	6	10	—	Bp Pt
Anemone quinquefolia	5	15	—	As Ta
Galium trifidum	5	40	—	Ps To
Gaultheria hispidula	5	35	—	Ab Pm
Pyrola rotundifolia	5	15	—	Pt Ab
Uvularia sessilifolia	5	20	—	As Ta
Arctostaphylos uva-ursi	1	80	1	Pr Ps
Smilacina trifolia	1	50	1	Ab To

* Plants in flower were *V. incognita*, *V. cucullata*, and *V. pallens*.

** Includes only the small, narrow-leaved sedges; the only plants in flower were *C. pensylvanica*.

Canopy trees:
Ab—*Abies balsamea*
As—*Acer saccharum*
Bl—*Betula lutea*
Bp—*Betula papyrifera*
Pm—*Picea mariana*
Pb—*Pinus banksiana*
Pr—*Pinus resinosa*
Ps—*Pinus strobus*
Pt—*Populus tremuloides*
Qb—*Quercus borealis*
Sa—*Sorbus americana*
Ta—*Tilia americana*
Tc—*Tsuga canadensis*
To—*Thuja occidentalis*

arranged in a linear continuum, many of the important relationships would have been disregarded. The stands on the wettest and driest sites have several shrub and herb species in common, indicating similarities in the two habitats in spite of great differences in moisture content of the soil. The center of the ordination is occupied by species that normally come in after disturbance, such as the two aspens and *Betula papyrifera*. Around the edges of the ordination are two distinct sequences leading from the pioneer forests, either wet or dry, to the sugar maple forests characteristic of the well-drained undisturbed upland habitats. The entire vegetation shows distinct patterns, apparently in response to the interrelations of the environmental factors of topography, soil, and drainage, and the historical factors of cutting, fire, and of fluctuations of the deer herd.

The Apostle Islands are unique in many respects. Their isolation, the absence of human habitation, and the differences in their history make them an ecological laboratory of unparalleled excellence. It is hoped that some of them may be preserved for further ecological studies.

SUMMARY

This study is a survey of the vegetation of the forests of the Apostle Islands, a group of 22 islands located in Lake Superior northeast of the Bayfield peninsula in Wisconsin.

Seventy-five stands were studied, covering the complete range of forest types on the islands. The most common forest type was dominated by either *Betula lutea* or *Thuja occidentalis*—often by both these species. Other important tree species were *Abies balsamea, Betula papyrifera, Populus tremuloides* and *Pinus strobus*. Important understory species were the shrubs *Taxus canadensis* and *Acer spicatum* and the herbs *Trientalis borealis, Maianthemum canadensis, Clintonia borealis*, and *Dryopteris austriaca*.

The stands were arranged in a three dimensional ordination. The ordination is discussed, and compared with other ordinations of the northern Wisconsin region.

ACKNOWLEDGMENTS

The field work for this project was carried out during the summers of 1956 and 1957. Appreciation is expressed to the following persons who aided in the collection of field data during these two summers: R. J. Vogl, J. R. Habeck, R. S. Cook, G. A. Curran, J. B. Hale, P. F. Maycock, D. J. Rogers, M. F. Vogl, and J. M. Tessaro. Drs. J. T. Curtis, H. H. Iltis, and P. F. Maycock helped in the identification of plant specimens. Jacqueline Miller aided in part of the computational work. Special thanks are due B. F. Waskow, O. Weborg, and C. Dahlstedt, of the Wisconsin Conservation Department at Bayfield, for their generous cooperation and assistance. Dr. J. T. Curtis has given invaluable aid in the planning and carrying out of this project.

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POLLEN STUDIES OF SOME TEXAS PEAT DEPOSITS[1]

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INTRODUCTION

The Pleistocene series is represented in Texas by sand and clay deposits of Beaumont and Lissie age, by stream terrace and lake deposits, and by numerous peat bogs. These bogs represent accumulations of partly decayed plant remains and usually contain large amounts of pollen preserved within their acid and anaerobic environment. Study of such pollen has contributed information important to considerations of climatic cycles and the disjunct distribution of certain plant communities (Sears 1942) and has been used in the correlation of glacial chronologies (Antevs 1955, Karlstrom 1956). Information from pollen analysis has also served as a basis for interpretations of paleoecology and glacial postglacial vegetational successions in the Pacific Northwest (Hansen 1947), Canada (Potzger and Courtemanche 1954), and Mexico (Sears 1952, Sears and Clisby 1955, Clisby and Sears 1955, Foreman 1955).

The first studies of pollen from Texas peat deposits were those of Potzger and Tharp (1943, 1947, 1954). These reflected vegetational changes from which modifications in climate were deduced and suggested, in particular, that the range of spruce and fir extended at one time into central Texas. The occurrence of boreal conifers far south of their present distribution would be an event of major ecological significance. This study supplements the work of Potzger and Tharp by analysis of the South Soefje bog. It is located near Ottine, Gonzales County, Texas, in the vicinity of Palmetto State Park (Fig. 1). Through the courtesy of Dr. Marion T. Hall, Butler University, material used by Dr. Potzger for analysis of a bog near Gause, Texas was available for re-study. In addition, material from a bog near Franklin, Texas (Potzger and Tharp

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[1] Taken from a thesis submitted by the first author in partial fulfillment for the degree of Master of Arts, The University of Texas. The authors gratefully acknowledge the support of the Humble Oil and Refining Company for this study.

1954), and from the North and South Soefje bogs (Fig. 1) was provided. Results of studies of the Soefje material were unpublished.

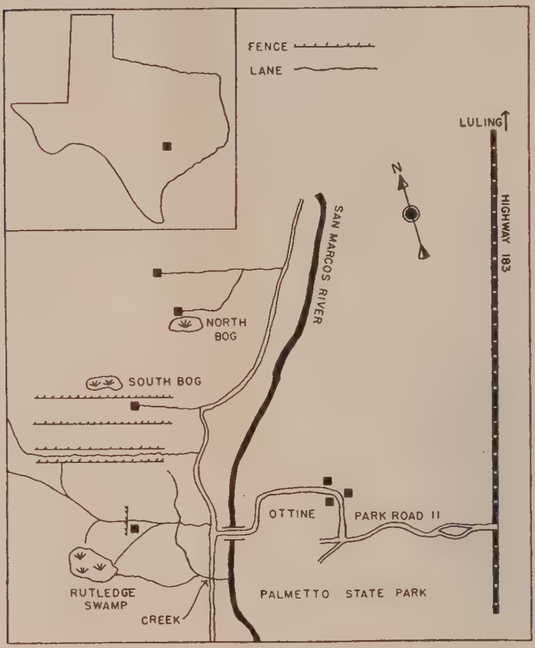

FIG. 1. Map of Soefje bog and adjacent area.

The South Soefje bog rests on the Carrizo (Eocene) formation. It exists under conditions typical of most peat sites in Texas, i.e., moderately high rainfall (35-45 in. per yr), rolling topography, and hillside location. The origin and structure of these bogs can be inferred through study of others in various stages of formation throughout East Texas. Water percolating through the pervious Carrizo sand stratum ultimately reaches impervious lower strata. It then spreads laterally and, in regions of rolling topography, eventually reappears at the surface along seepage lines on hillsides. Hydrophytic vegetation developing near these seepages receives additional water by surface drainage from the upper portions of the slope. Plants grow rapidly in such localities when there is enough rainfall for a continuous flow of water, and from their remains peat is formed. The depth to which the peat can accumulate depends on the topography. In the South Soefje bog it has accumulated to 4.7 m in a depression at the base of the sandy hill, from which seepage water collects over bedrock or impervious clay.

MATERIALS AND METHODS

Peat for this study was obtained by use of a Hiller borer. The core was divided into 5 cm segments and placed in labeled vials. A portion of peat from every other vial (10 cm increments) was prepared by a modification of the acetolysis treatment described by Faegri and Iversen (1950). Samples from the lower 5 ft of the Gause bog were processed by the same procedure from material originally sent to Dr. Potzger by Dr. B. C. Tharp in 1942. Some of the latter samples were dry, but counts were obtained from all levels. These counts were made (1) to verify the presence of *Abies, Picea,* and *Castanea* pollen; (2) to substantiate the high percentages of *Alnus* pollen reported for the Gause bog before attempting to interpret the Soefje profile; and (3) to provide another profile for comparison and correlation.

A preliminary analysis of the samples from the Soefje bog indicated that the number of different pollen and spore types and their distribution at different levels were such that counts of 200 (Barkley 1934) would reflect adequately the vegetational sequence of the area as represented by the pollen flora of the bog. Counts based on 200 tree pollen (AP) were also made to magnify trends not evident from the count based on total pollen and spores.

Single grain mounts, prepared according to the method of Faegri (1939) were utilized in identification procedures. Although these are not widely used in pollen studies of Pleistocene deposits in America, they are important as voucher specimens for identifications that are made. In a permanent collection they are accessible to workers desiring refinement or verification of a specific study. Such mounts also facilitate later recognition of unknown pollen and spores. In addition, selection of material in any sample for single grain mounts involves more extensive inspection than is customarily practiced in making the standard 200 grain counts; thus more exact qualitative evaluations are possible. Lastly, peat bogs are often destroyed by commercial peat companies and it is desirable to have representative specimens in a permanent collection. All deposits from which Potzger and Tharp reported spruce and fir pollen have been destroyed by commercial operations.

Before studying fossil pollen, it is essential to establish a collection of Recent pollen preparations. Permanent slides of 1100 specimens, including those grains used for comparison, were prepared by the KOH-acetolysis technique. The materials of this study, including the permanent slides, are in the pollen collection of The University of Texas Herbarium.

The terminology for describing features of pollen and spore morphology is from Iversen and Troels-Smith (1950).

The photomicrographs were made from single grain mounts with an Orthophot camera and illuminator. The microscope was equipped with a 1.30 N. A. apochromatic oil immersion objective, a 1.30 N. A. condenser and compensating eyepieces.

RESULTS

The Soefje Bog

Present Vegetation.—Comprehensive lists of plants in Palmetto State Park have been given by Bogusch (1928) and Parks (1935). Tharp (1939) designated the general vegetation of the area as an Oak-Hickory association. The dominant trees are *Quercus stellata* Wang. (post oak), *Q. marilandica* Muench. (black-jack oak), and *Carya buckleyi* var. *arkansana* Sarg. (hickory). Minor associated tree and shrub species are *Q. virginiana* Mill. (live oak), *Q. macrocarpa* Michx. (bur oak), *Ulmus americana* L. (American elm), *Salix nigra* Marsh. (black willow), *Vaccinium arboreum* Marsh. (huckleberry), *Myrica cerifera* (L.) Small (wax myrtle), *Ilex decidua* Walt. and *I. vomitoria* Ait. (yaupon), and *Lyonia mariana* (L.) D. Don (stagger-bush). *Fraxinus pennsylvanica* Marsh. (ash) was abundant around one bog in the area but has since been eradicated and is now confined chiefly to creek bottoms. Ferns and mosses are represented by *Osmunda cinnamomea* L. (cinnamon fern) and *Sphagnum subsecundum* Nees (peat moss).

The distribution of other species no longer growing near the Soefje bog has been noted in relation to the pollen study. These are mostly anemophilous. Pines, common in East Texas, occur in isolated stands at Bastrop (Bastrop County) north of Columbus (Colorado County), near Bellville (Austin County), at Navasota and Singleton (Grimes County), and northeast of Huntsville (Walker County). These stands are 40 to 145 miles from the Soefje bog. The species represented are *Pinus echinata* Mill. (short leaf pine), *P. palustris* Mill. (long leaf pine), and *P. taeda* L. (loblolly pine). The Soefje bog is probably within the range of pollen distribution from most of these stands. *Liquidambar styraciflura* L. (sweet gum) grows in eastern Texas

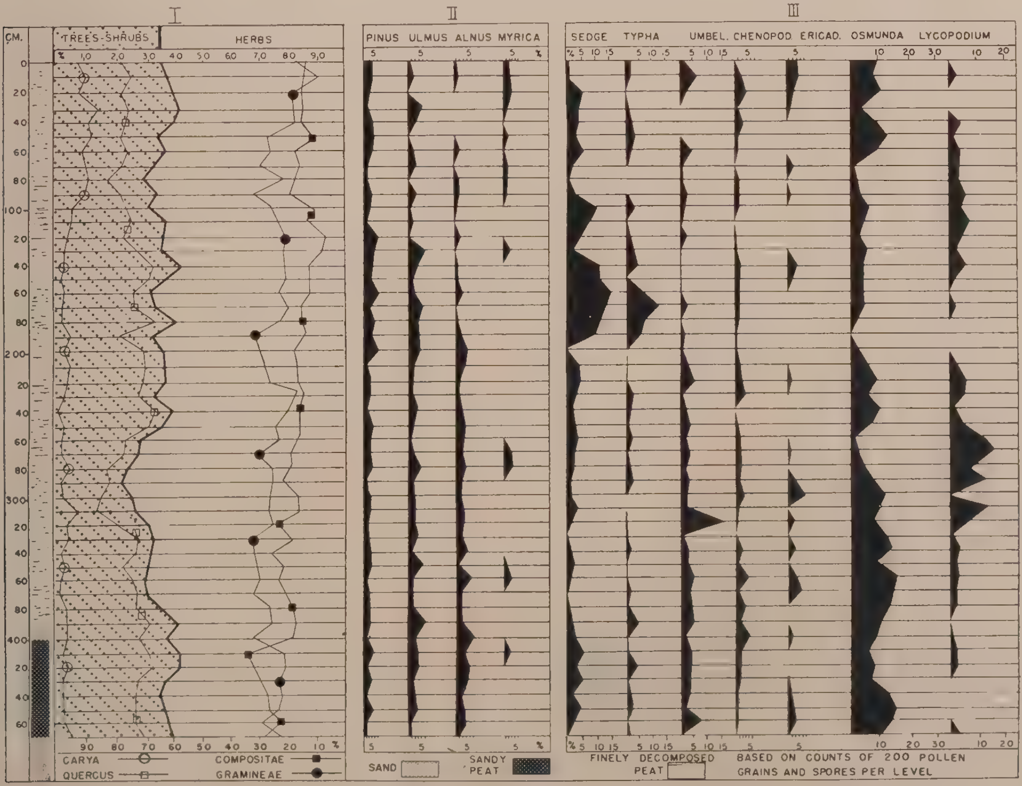

FIG. 2. Pollen diagram of the south Soefje bog. Based on counts of 200 pollen grains and spores from 47 samples processed at 10 cm intervals. (See text for further explanation.)

approximately 100-150 miles northeast of the Soefje bog (40 miles northeast of the Gause bog). *Alnus rugosa* (DuRoi) Spreng. (alder) grows along creeks and small tributaries of the Trinity River in the same vicinity. *Drosera rotundifolia* L. (sundew) has been found near the bog, although it was rare or absent there at the time of the study.

Pollen and spores of certain plants anticipated to be present in the bog were not encountered. *Prosopis juliflora* var. *glandulosa* Cockerell (mesquite) and *Juniperus virginiana* L. (cedar) grow in the region, although not in the park area. *Sphagnum subsecundum* has been collected from the surface of the bog. The absence of spores of this species of *Sphagnum* may be accounted for by the fact that the exospore has little resistance to the chemical effects of the acetolysis treatment and is easily corroded (Faegri and Iversen 1950, p. 120). *Ilex* and *Myrica* pollen was not abundant, but both are insect pollinated and produce only small amounts of pollen. The remainder of the dominant elements in the flora were represented by pollen.

The Pollen Diagram.—The pollen diagram of the South Soefje bog (Fig. 2) represents percentages of pollen and spores based on counts of 200, including unknowns, from 47 samples processed at 10 cm intervals.

As each cylinder of peat was removed from the bog, the presence of sand and the degree of decomposition of peat were noted. These features often indicate the climatic environment during which a given portion of peat was formed. Prolonged drought results in outwash of sand from the upper portions of the slope, preserving in the bog lithologic evidence of xeric conditions. The absence of interspersed sand layers and the uniform character of the peat suggest that there were no marked environmental changes during its deposition.

The results of the pollen and spore counts are in columns I, II, and III of Figure 2. Column I shows the relative abundance of tree and shrub pollen compared to that of herbs. Individual curves for pollen of *Carya, Quercus, Gramineae,* and *Compositae* are also given. Column II indicates the percentages of minor associated tree pollen. The percentages of spores and of pollen of herbaceous plants present in small quantity are in column III. The distribution and percentages of pollen grains not present in sufficient quantities to be included on the diagram are in Table I. Table II represents the distribution and percentages of unknown grains.

TABLE I. Distribution of pollen grains not present in sufficient quantities to be included in the pollen diagram

Level in cm	Malvaceae	Onagraceae	Polygonaceae	Drosera	Galium	Gaura	Juglans	Liquidambar	Salix	Vitis
0			1		8		1		1	
10										
20			1						1	
30										
40										
50										
60										
70			1						1	
80				1						
90										
100					1	1				
110				3						1
120				2	1					
130										
140				3	2				1	1
150										
160			1	2						
170										1
180				3						
190				3						
200				4						
210										
220	1									
230										
240										
250										
260										
270		2								
280						2				
290		3			1	1				
300									2	
310	1									
320						1				
330										
340										
350										
360					2	2				
370										
380										
390										
400								1		
410										
420										
430										
440										
450										
460										
470						1				

In contrast to the marked changes in vegetation indicated by pollen analysis of the Gause, Patschke, and to a lesser extent, the Franklin bog (Potzger and Tharp 1947, 1954), the pollen profile of the Soefje bog reflects an essentially unmodified vegetation. *Quercus* pollen (Fig. 3, F) constitutes approximately 20% of the total pollen and spores in the lower portion of the bog. This percentage persists to the surface level with only minor fluctuations, indicating that oaks have been dominant in the flora for a time equal, at a minimum, to the age of the Soefje bog. Grasses (Fig.

Table II. Distribution of unknown pollen grains in the Soefje bog

Level in cm	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	Total (%)
0											3	3	1								8	3	9
10	2	1		4	3	2		1			3			2					1		2		11
20	3	2		1		2					3			2							4		9
30				4										1							4		5
40											2			2					2				3
50						1		1			2			2							3		5
60								1			3			2							3		5
70	2							1			1			1			2				2		5
80			2	5		2		2			1					1					2	2	9
90	3			8			1													1			7
100																					2		1
100		1				1		3			2												4
120				2	1	2								1					1		1		4
130				8	3	1					1	1							3		4		11
140				1	2						2										3		4
150		1				1					2												2
160								2							1						1		2
170		2									2										1		3
180				8																	3		6
190			2			3					1						1						4
200		1	1								1												2
210		1				2			2		1	1									1		4
220											3	2									1		3
230											2										15		9
240							2												3		3		4
250	2		2	2	1	2													1		4		7
260				2																	11		7
270					2				1										1		9		7
280						1												1		2	3		4
290	3	1																			3		4
300				2		2				2	2										1		5
310																							0
320				2			1			2	15				1				3		1		13
330							2			1	3												3
340											5												3
350			1	2	1						3				1						2		5
360	2	2			1						1				2						3		6
370	1				1					1	2									2			4
380						1													1				1
390	2		1			1									1						3		4
400	1	2		2					1		1		1		1							2	6
410		4		1							1				1							2	5
420	2	1													1								3
430	1										1		1		3								3
440		1					1						1										2
450	2	1					1		1		2				3								5
460																							0
470																							0

4, A) and members of the Compositae (Fig. 4, H-K; Fig. 5, A, B) each constitute approximately 20% of the pollen and also show no significant variation in abundance. Pollen of *Pinus* (Fig. 3, C), *Ulmus* (Fig. 3, I), *Alnus* (Fig. 3, D), and *Myrica* (Fig. 3, L) do not exceed 5% and are present at most depths.

Although marked changes in the vegetation are not suggested, fluctuations in the abundance of several pollen types are found at different levels. Sedge pollen (Fig. 4, C) is abundant between the one and two meter depths; its poor representation at other levels probably reflects variations in the microclimate, since other elements in the profile characteristic of moist conditions do not change accordingly (i.e., *Typha* and ferns). The Umbelliferae (Fig. 5, C-F) are represented by a pronounced maximum of 15% at the 3.2 m level but do not show further marked variations. *Osmunda* (Fig. 3, B) and *Lycopodium* (Fig. 3, A) range widely in amount; the former is generally more abundant at intermediate and lower depths and the latter is most numerous at intermediate levels. *Carya* pollen (Fig. 3, J), present in small percentages in the lower levels, increases slightly in the upper meter. This trend was noted by Potzger and Tharp (1954) in the Gause bog. Pollen of the Chenopodiaceae (Fig. 4, D) and Ericaceae (Fig. 4, G) is present in small amounts throughout most of the profile.

Juglans (Fig. 3, K), *Liquidambar* (Fig. 3, E), and *Salix* pollen was not abundant. The pollen of minor associated herbs, such as the Malvaceae (Fig. 4, E) and the Onagraceae (Fig. 4, f; Fig. 5, G) was also distributed fairly equally through all levels (Table I). *Drosera* (Fig. 5, H), however, is mostly confined to the one to two meter level and certain other types, i.e., the Polygonaceae (Fig. 4, B), are characteristic of only a certain section of the profile. These few types are, however, insufficient in amounts to warrant interpretations of vegetational changes based on their occurrence.

Twenty-two unknowns were encountered while tabulating spores and pollen from the Soefje bog (Table II). The maximum percentage of unknowns was 13 at the 3.2 m level with an average of approximately 4%. The significance of the distribution of these unknowns is uncertain, although apparently certain types, such as N and O, are restricted to specific portions of the profile and thus may be of some value in correlating levels of the Soefje bog with others in the region.

Pollen and Spore Identification.—Certain pollen and spore types in the Soefje bog are difficult to identify. The spores of *Osmunda* when split along the triradiate scar resemble the pollen of *Nymphaea,* and some of the latter may have been included with *Osmunda.* A triradiate scar was visible on each intact spore, however, and *Nymphaea* is not known to occur near the bog. If *Nymphaea* pollen is present, its percentage is small. The pollen tetrads of some species of *Typha* are readily identified, whereas the monadal grains of other species are difficult to distinguish from those of *Sparganium.* The identification of single-grain types such as *Typha* is arbitrarily based on the presence of this genus in the surrounding area, whereas *Sparganium* is absent.

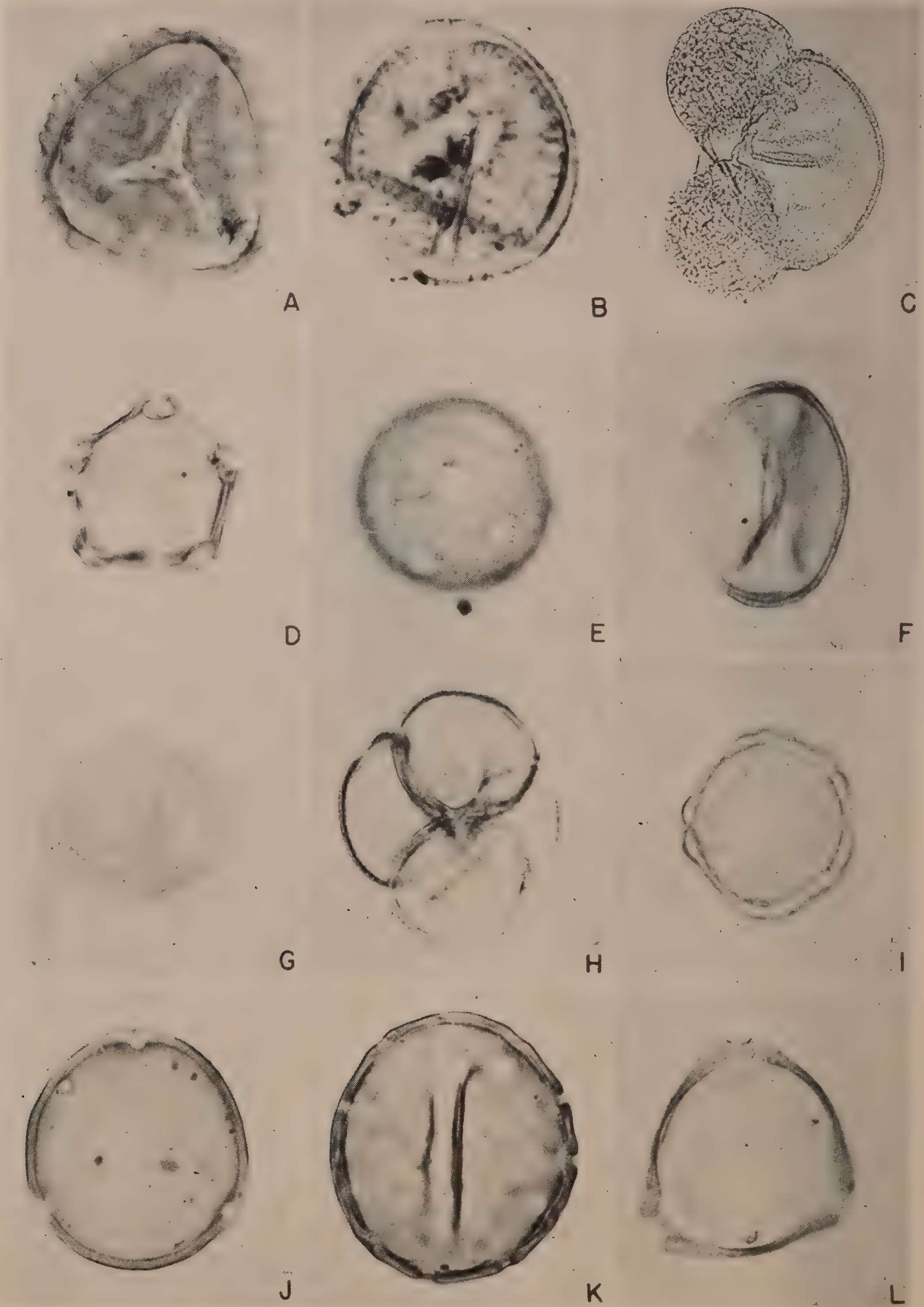

FIG. 3. Photomicrographs of pollen and spores from the south Soefje bog. The actual size, given in microns, represents the greatest diameter. Figures in parentheses represent levels of focus as defined by Iversen and Troels-Smith (1950).

A. *Lycopodium*	57 μ (5)
B. *Osmunda*	59 μ (4)
C. *Pinus*	99 μ (5)
D. *Alnus*	30 μ (5)
E. *Liquidambar*	36 μ (2)
F. *Quercus*	36 x 29 μ (5)
G. *Typha angustifolia* L.	36 μ (2)
H. *T. latifolia* L.	45 μ (5)
I. *Ulmus*	31 μ (4)
J. *Carya*	46 μ (5)
K. *Juglans*	45 μ (5)
L. *Myrica*	27 μ (5)

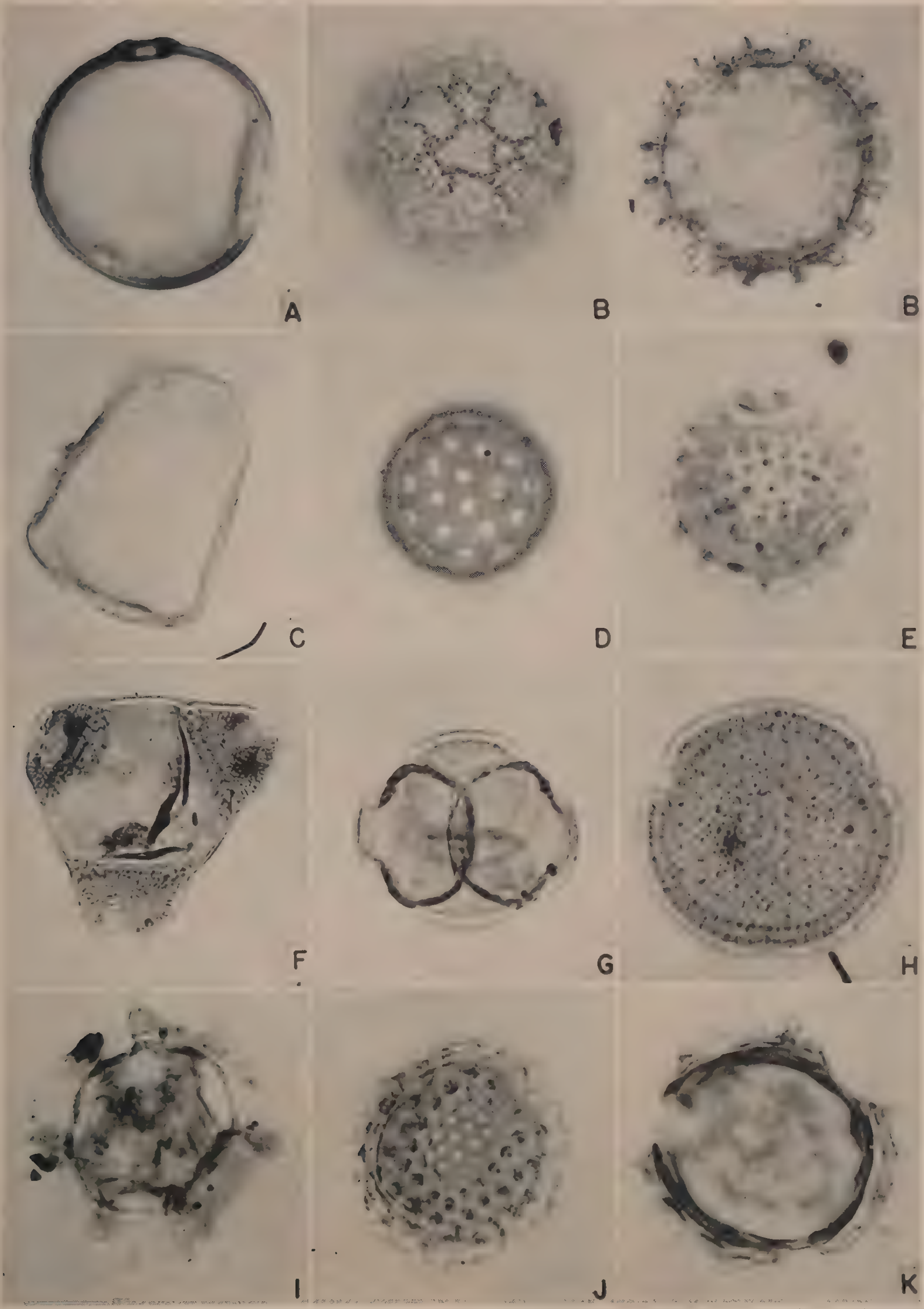

FIG. 4. Photomicrographs of pollen grains from the south Soefje bog. See Fig. 4 for further explanation.

A. Gramineae	41 μ (5)	E. Malvaceae	36 μ (4)	I. Compositae	44 μ (3)
C. Cyperaceae	44 x 33 μ (5)	H. Compositae (?)	31 μ (5)		
D. Chenopodiceae	24 μ (2)	G. Ericaceae	45 μ (5)	J. Compositae	27 μ (4)
B. Polygonaceae	42 μ (3,5)	F. Onagraceae	81 μ (5)	K. Compositae	40 μ (5)

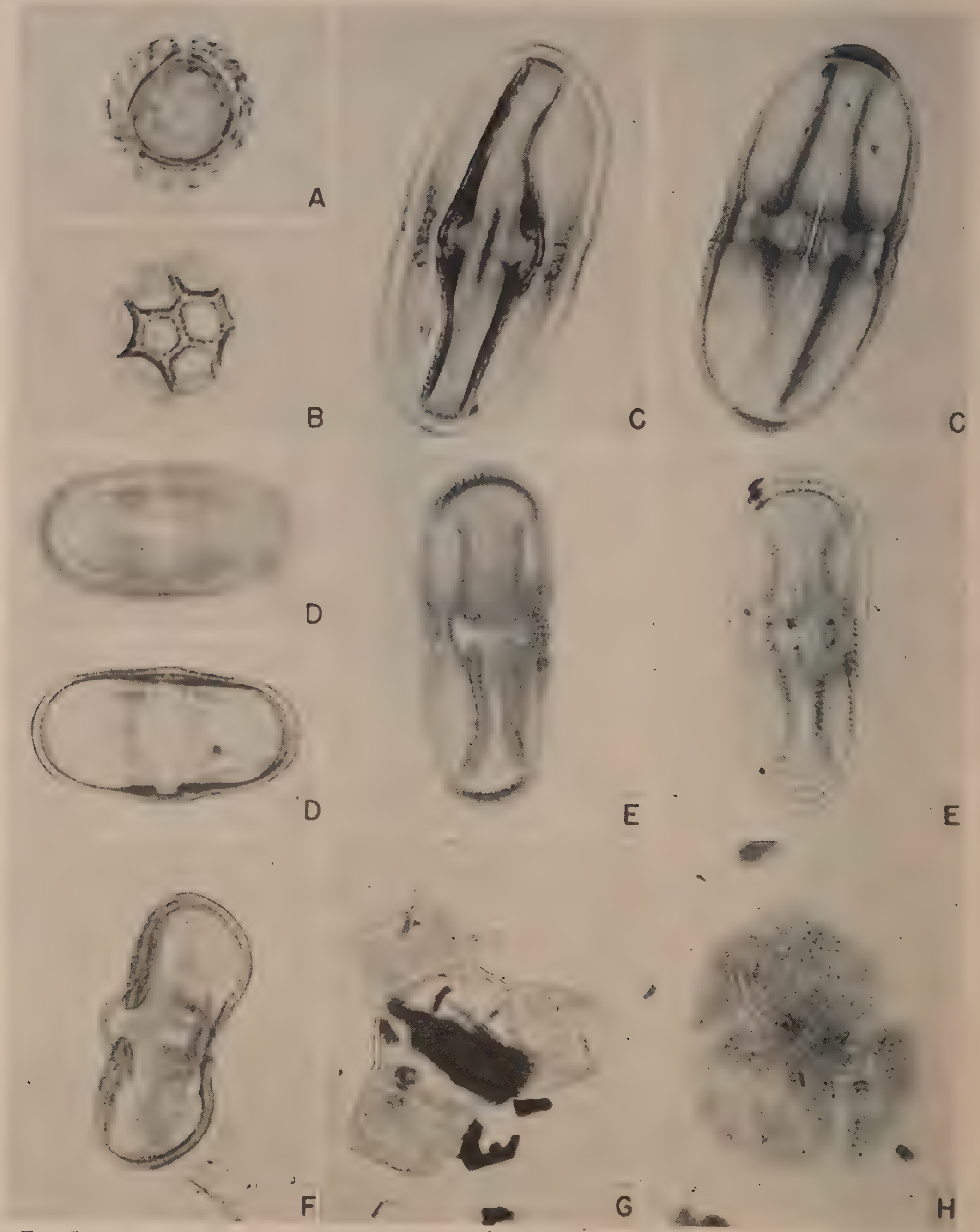

FIG. 5. Photographs of pollen grains from the south Soefje bog. See Fig. 4 for further explanation.

A. Compositae	21 µ (5)	D. Umbelliferae	30 x 16 µ (3,5)	G. *Gaura*	90 µ (5)
B. Amaranthaceae (?)	21 µ (3)	E. Umbelliferae	40 x 24 µ (3,5)	H. *Drosera*	49 µ (4)
C. Umbelliferae	58 x 27 µ (3,5)	F. Umbelliferae	42 x 21 µ (5)		

There is no satisfactory method for distinguishing pollen of grass genera (Geisler 1945). If there are relatively few genera, distinctions based on pore-axis ratios may be possible (Barghoorn, Wolfe and Clisby 1954). Measurements of this type on grass pollen in the Soefje bog intergraded to such an extent that generic differentiation was not possible.

It is also difficult to distinguish pollen of various species of *Quercus*. Slides of recent species were grouped first according to subgenera (Lepidobalanus, the white oaks, and Erythrobalnus, the red and black oaks) and then according to ecological requirements, (i.e., those species which grow in moist habitats and those which grow under more xeric conditions). There was no consistent correlation of oak pollen characteristics with either the systematic or ecological grouping of the species.[1]

The pollen of *Pinus* can be separated into two morphological groups, the Haploxylon-type with the bladders appearing as hemispheres in polar view and the Sylvestris-type which in polar view appears as 3 overlapping circles (Rudolph 1935). Size variations occur in each group, and sometimes it is possible to distinguish certain *Pinus* species using size statistics (Cain 1940). However, as shown by Cain and Cain (1948) pollen size can vary with differences in the environment under which the species is growing. Buell (1946) showed that pine pollen from herbarium sheets swells to a greater size than fossilized pine pollen during treatment. The size of some conifer pollen also varies with the method of treatment (Cain 1944). No attempt was made in this study to identify the species of pine pollen using size statistics and no significant trends were noted in the distribution of morphological types throughout the profile.

Myrica pollen can be distinguished from that of *Corylus, Ostrya*, and *Carpinus* by several features, one of which is the dentations on the inner surface of the exine in the region of the pores (Wodehouse 1935, p. 363). Separation of the endexine from the ectexine at the pore is a distinguishing feature for pollen of *Myrica* and one apparently less susceptible to obliteration during fossilization.

The Radiocarbon Date.—The principles upon which age determinations by radiocarbon content are based have been reviewed by Libby (1955). Antevs (1953, 1955, 1957) felt that the chemical reactions in peat bogs were capable of altering the C^{14} content of peat to the extent that many dates from such sources are inaccurate. The Two Creeks Forest Beds and the Cochrane Moraine which he discussed are cited as examples of the use of C^{14} dates in conflict with varve chronologies and synchronization of major climatic cycles in America and Europe. Acknowledging the possible error in any specific date, Johnson (1955) and others expressed the opinion that the technique is accurate within the limits of error given with each date and that the method can yield valuable information on problems of Pleistocene chronology and history.

A radiocarbon date of 7,820 ± 350 yr was determined for peat from the bottom of the South Soefje bog. This determination was made by the Exploration Department Geo-chemical Laboratory, Humble Oil and Refining Company as run number 0-501.

The results of a comparison between pollen and spore types recognized in the Soefje bog with extant vegetation nearby suggests a high degree of stability for the composition of plant communities in Palmetto State Park. Not only are the same pollen types represented throughout the pollen diagram, but the relative proportion of the various types has remained essentially constant. Thus both qualitative and quantitative considerations suggest that the region including Palmetto State Park has provided a stable environment for the plant communities present for approximately 8,000 yr.

The Gause Bog

Results from the study of the Soefje bog have been compared with those reported by Potzger and Tharp (1954) from the Gause bog. The presence of 11% *Abies* and *Picea* pollen at the 13-13.7 ft level of the Gause bog and subsequent changes in pollen types were interpreted by these authors as reflecting a succession of climatic changes in the order of cool-moist, dry, warm-moist, and warm-dry as at present. Such an interpretation would not be warranted by the pollen analysis of the Soefje bog.

Several factors may account for the differences in results of the two studies. First, possibly climatic successions resulting in changes in the vegetation, as reflected by the pollen analysis of the Gause bog, were completed before the Soefje bog began to form. If this were correct, the lowermost level of the Soefje bog would correlate with the Gause bog at some point above the 9 ft level, since it is here that climates of the present are first suggested by the Gause profile.

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[1] Grateful acknowledgment is made to Dr. C. H. Muller for outlining the ecological requirements of the several species of oaks.

Second, although climatic changes were occurring near Palmetto Park after the initiation of peat formation in the Soefje bog, these changes may not have altered the vegetation in the area significantly. During the recent prolonged drought which affected vegetation in many parts of Texas, the composition of plant communities at Palmetto Park was not changed appreciably. The physiographic structure of the region may modify any effects of climatic change so that the plant communities are provided with a relatively stable environment.

Thirdly, interpretations based on certain aspects of the Gause profile may warrant some revision. It was possible to evaluate each of these possibilities by the availability of material from the Gause bog.

Pollen from the lower 5 ft of the Gause bog was counted by the same procedures used for the Soefje bog and also on the basis of the pollen types recognized in the original analysis by Potzger (Potzger and Tharp 1954). Results of the counts by these two procedures are in Tables III and IV. The following may be noted from counts based on 200 pollen grains and spores (Table III): (1) *Picea* pollen constituted 2% of the total pollen and spores, (2) the presence of *Castanea* pollen could not be verified, and (3) the percentages of oak, grass, and *Alnus* pollen differed markedly from those in the original analysis. Counts based on the pollen types recognized in the earlier study (Table IV) indicated a slightly greater amount of *Picea* pollen (3%), the absence of *Castanea* pollen, and simliar differences in abundance of oak, grass, and *Alnus* pollen in comparison with the original report.

TABLE III. Tabulation of pollen grains and spores from the Gause bog based on a count of 200[1]

	LEVELS IN FEET				
	10-11	11-12	12-13	13-13.7	13.9-14
Abies	0	0	0	0	0
Alnus	65	61	52	31	34
Carya	4	3	1	3	2
Castanea	0	0	0	0	0
Corylus	3	2	4	3	8
Myrica	4	0	1	0	0
Picea	0	0	0	3	0
Pinus	2	3	3	8	5
Quercus	20	20	14	21	22
Ulmus	1	2	0	0	0
Chenopodiaceae	0	3	1	1	2
Compositae	20	28	28	28	32
Cyperaceae	32	2	0	22	21
Gramineae	35	20	9	10	40
Lycopodium	0	0	0	0	2
Nymphaea	0	0	0	4	3
Onagraceae	0	0	1	0	0
Osmunda	3	6	2	2	2
Polypodium	2	25	70	31	24
Other Spores	0	2	0	5	0
Typha	0	4	3	0	1
Umbelliferae	1	6	3	6	2
Unknowns	8	13	8	21	0
Totals	200	200	200	200	200

[1] Trees and shrubs are listed separately from herbs in the table, but both were included in the tabulation.

TABLE IV. Tabulation of pollen grains and spores from the 13-13.7 ft level of the Gause bog[1]

	First Count	Second Count	Third Count
Abies	0	1?	0
Alnus	74	70	78
Betula	2	0	2
Carya	11	15	13
Castanea	0	0	0
Corylus	7	5	8
Gramineae	28	25	24
Myrica	6	4	5
Ostrya	1	2	0
Picea	5	4	6
Pinus	23	29	22
Quercus	43	45	42
Total	200	200	200
Chenopodiaceae	3	3	2
Compositae	50	62	61
Cyperaceae	30	36	29
Onagraceae	0	2	0
Osmunda	12	12	11
Other Spores	4	9	6
Polypodium	50	71	65
Typha	1	1	2
Umbelliferae	10	8	7
Vitis	0	1	0
Unknowns	28	21	26

[1] Counts were based on the pollen types used in the original analysis (trees, shrubs, grasses). Other pollen grains and spores, not included in the counts of 200, are listed separately.

Although these results verify the presence of *Picea* pollen in the Gause bog samples, it was less abundant than originally reported.

For identification of *Castanea* pollen, reference preparations were made from herbarium specimens of *C. pumila* (L.) Mill. (chinquapin), the only species growing in Texas, and *C. dentata* (Marsh.) Borkh. (American chestnut); these were checked against several descriptions and illustrations in the literature. During preliminary examination of the samples occasional tricolporate grains were found that were similar in size to *Castanea*. The very low percentage of these grains throughout the profile suggests wind dissemination from some plant nearby. *Castanea* presently grows in East Texas.

Differences in the amounts of oak, grass, and *Alnus* pollen are significant, for variations in the amount of pollen from these genera (with *Castanea*) served as the basis for the suggested climatic changes in central Texas. In the original analysis of the Gause bog, *Quercus* pollen comprised about 10% at the 13-13.7 ft level. Using the same material and the same basis for tabulation, Table IV shows that the minimum percentage of oak pollen recognized in 3 separate counts was 21%. The percentage of *Alnus* pollen was reported as somewhat less than 10% at the same level; this study indicates that *Alnus* pollen represented at least 35%. The most marked difference concerned the amount of grass pollen. The original report suggested that grass pollen constituted about 55% of the total at the 13-13.7 ft level. Table IV indicates a maximum of 14% for the pollen of grasses at this level. High percentages of Cyperaceae pollen are present, and it may be that some of these grains were included in the grass pollen percentages. These differences were of such magnitude that a fourth count, not included in Tables III and IV, was made to verify the first 3 tabulations. The results agreed with the 3 earlier findings.

During the tabulations a few fragments of a conifer pollen grain were found which could not be identified with certainty and may have represented *Abies*. However, examination of the samples from the 13-13.7 ft level, wherein several hundred grains were counted, did not reveal any pollen type that could be positively identified as *Abies*.

Occasional grains of the Rosaceae, *Juniperus, Ilex, Galium,* and *Acer* were present, but were not encountered in the tabulations.

Certain samples from the Gause bog were dry, and this suggests that deterioration could account for the differences in results of the two studies. This is not probable, however, since the sample from the 13-13.7 ft level was still moist and, in addition, a greater number of pollen types were recognized than reported originally. It is not likely that deterioration would have completely destroyed all the relatively resistant pollen of *Castanea* and *Abies,* leaving the remaining types intact and uncorroded. The fact that the acetolysis technique was used to prepare samples from the Gause bog, whereas Potzger used the Geisler (1936) method, would not account for the absence of *Castanea* or *Abies* pollen, since these types are often present in peat samples processed by the acetolysis technique.

DISCUSSION

Late Pleistocene Climates in Central Texas: An evaluation of the possible climatic changes in central Texas during the late Pleistocene presents numerous problems. First, it is necessary to differentiate between those aspects of a pollen diagram which deserve emphasis in such considerations and those which may not always be critical. The migration of a species into an area can be interpreted as reflecting changes in the climate favoring the growth of that species. The climatic change necessary to support such a migration would probably be of greater magnitude than that required to produce changes in the abundance of plants normally present in the area. Changes of the latter type can often be attributed to variations in the microclimate. Even when there are pronounced fluctuations in the abundance of certain plants, as for example, oaks, grasses, and composites, critical evaluations of the climatic significance of such changes, when reflected by a pollen diagram, are difficult since species in these groups cannot, at present, be segregated into xerophytic, mesophytic, and hydrophytic types on the basis of pollen characteristics.

Second, in the original pollen analysis of samples from the Gause bog (Potzger and Tharp 1954), 11% *Abies* and *Picea* pollen was reported. Pine, which is a notable producer of large amounts of pollen, presently grows within 40 miles of the bog and contributed less than 5% pollen. Since *Abies* and *Picea,* which normally produce less pollen than pine, contributed from two to three times as much, it seems reasonable to assume the presence of spruce and fir in some abundance. The occurrence of large stands of spruce and fir near the bog would have significant implication concerning (1) the magnitude of climatic changes occurring in central Texas and (2) the distance involved in the displacement of these boreal elements to the south. Correlated variations in abundance of pollen of grasses, oaks, *Alnus,* and *Castanea* in the original analysis formed the basis for the interpretation that there were later climatic changes which affected the distribution of major vegetational elements.

This study indicates that *Picea* pollen was less abundant (3%), that pollen of *Castanea* and possibly *Abies* was absent, and that reported changes in the percentages of *Alnus,* oak, and grass pollen need revision. These findings do not suggest an extensive boreal coniferous forest in central Texas during relatively recent time nor do they indicate climatic changes of great magnitude. A re-evaluation of the interpretation of late Pleistocene climates in central Texas suggests that the proposal of a four-phase climatic oscillation (Potzger and Tharp 1954) is not supported by present information and that a more flexible interpretation is desirable. The pollen content of the lower levels of the Gause bog suggests a climate cooler and wetter than at present. Subsequent changes in the Soefje and Gause profiles are interpreted to indicate a gradual, progressive trend toward present climatic conditions.

A Date for the Spruce Period.—To determine the time at which spruce persisted in Texas, an extensive, though unsuccessful, search was made for other bogs containing spruce pollen with the intention of obtaining material suitable for radiocarbon dating. The failure to obtain such peat material made it necessary to consider other possibilties for establishing the time during which spruce existed in or near central Texas. Two sources of information were available for this purpose: first, a correlation of the bottom level of the Soefje bog, known to be approximately 8,000 yr old, with some level of the Gause bog, then extrapolation to the level of spruce pollen; second, correlation of the disappearance of spruce pollen from the Gause bog with glacial and other climatic events which have been dated. Neither of these sources of information can be considered accurate in itself, but agreement in the results from these different approaches could be of value.

The lower level of the Soefje bog would probably correlate with the Gause bog at some point near the 9 ft level in the latter where the two pollen profiles first correspond. Assuming an age of approximately 8,000 yr for the 9 ft level of the Gause bog, an average rate of peat formation of one foot per 900 yr is obtained. This would date the 13.7 ft level of the Gause bog at approximately 12, 230 yr.

The second approach to the problem of age determination is attributable to Dr. Ernst Antevs. Prior to the availability of the above estimate, Antevs (personal communication, April 15, 1957) made this suggestion concerning the time at which spruce (and fir) presumably occurred in Texas:

> For correlation purposes the principal climatic change recorded in the Patschke and Gause bogs seems to be the extinction of spruce and fir and increase of oak and *Castanea* at the depths of 17.5 and 13 feet. This temperature rise seems to be the best starting point for correlating the bogs with the glacial history, and it is probably the Texas correlative of the marked general late-glacial temperature increase.
>
> I refer to the general temperature rise which began in Europe with the Alleröd age and in Canada during the Timiskaming ice retreat. Varve dates: about 12,500 B.P. (Before Present). Radiocarbon date of the Alleröd in Denmark: 12,000-10,800 B.P. The same marked temperature increase is recorded in deep-sea sediments in the Atlantic and the Carribean; its beginning has been radiocarbon dated at roughly 13,000 B.P.
>
> I would, therefore, date the extinction of boreal pollen in your bogs at roughly 12,500 B.P.

From these different types of evidence it appears that the last spruce pollen was deposited in the Gause bog approximately 12,500 yr ago. Because this age estimate was obtained indirectly, however, and because the Alleröd-Timiskaming correlation suggested by Antevs is not accepted by many North American Pleistocene geologists, it is desirable to consider additional data in evaluating the validity of this date. Pertinent evidence is derived from a consideration of the glacial and climatic events to the north at the time spruce appears to have been eliminated from Texas. According to Horberg (1955) the Cary ice sheet was well in retreat 12,500 yr ago, indicating a definite trend toward warmer climates. If it is assumed that spruce was near the southern limit of its range in Texas, then its disappearance from this area might be expected during the period of climatic amelioration. Thus there seems to be some geologic evidence to favor a date of 12,500 yr for the final spruce pollen in the Gause bog although it is obvious that a number of variables may affect the accuracy of this estimate.

SUMMARY

Pollen in peat from the south Soefje bog (4.7 m deep) Gonzales County, Texas, was studied to correlate findings with those of Potzger and Tharp (1947, 1954) who studied material from the Patschke (6.8 m deep), Gause (4.1 m deep), and Franklin (3 m deep) bogs in Lee, Milam, and Robertson Counties, respectively. Samples from the lower 5 ft of the Gause bog were also studied. Samples were processed by the technique suggested by Faegri and Iversen (1950) and counts of 200 pollen grains and spores, including unknowns, were made at 10 cm intervals.

Findings from the Soefje bog suggest a high degree of stability of the plant associations near Palmetto State Park, and a radiocarbon date (7,820 ± 350 yr, run 0-501, Humble Oil and Refining Company) from the bottom level indicates that this stability has persisted for approximately 8,000 yr.

In contrast to results obtained from the original analysis of the Gause and Patschke bogs, the pollen profile of the Soefje bog and the results of the re-examination of the Gause bog material do not form a basis for deducing, during the period of bog formation, major climatic changes in central Texas or for (1) postulating the presence of large stands of spruce and fir in the area or (2) a relatively recent migration of these boreal elements into central Texas. Pollen analysis and other information correlated with it suggest that

spruce, possibly isolated during an earlier period of more significant climatic changes, existed near the bog until approximately 12,500 yr ago, reflecting a relatively cool and moist climate at that time; subsequent changes in the pollen profiles are interpreted to indicate a gradual change through a warm-moist period to the warm-dry climate that now exists.

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EFFECTS OF *HALOGETON GLOMERATUS* LEACHATE ON CHEMICAL AND PHYSICAL CHARACTERISTICS OF SOILS[1]

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Livestock grazing and attempted dry-land farming have depleted many rangelands and left others denuded of desirable perennial vegetation. *Halogeton glomeratus* (M. Bieb) C. A. Mey., a poisonous, annual weed, has invaded some depleted rangelands in the Western United States and now occupies vast acreages, frequently in dense, pure stands.

On some areas of former salt-desert types in eastern Nevada the entire plant cover consists of halogeton (Fig. 1). Whether these areas were denuded originally by overgrazing, farming, insects, or other factors is not known. Abandoned town sites support dense stands of halogeton. Experimental seedings made in halogeton-infested areas generally have failed. Even more striking is the lack of reinvasion by adjacent native species. The soil-plant relations in these halogeton stands are complex and have received little study.

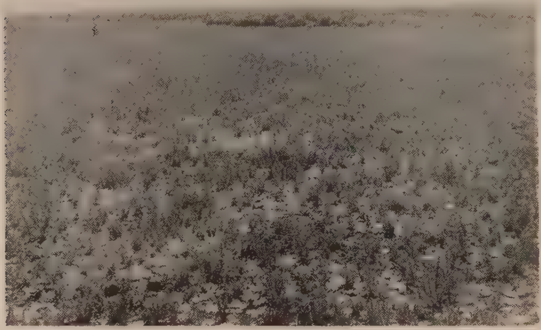

Fig. 1. A range area in eastern Nevada denuded at some time in the past and now supporting a dense stand of halogeton.

Soil salinity and low precipitation restrict water availability to plants in the salt-desert type. If halogeton imparts additional salts to the soil surface, the chemical and physical characteristics of the soil may be changed to impair germination and growth of desirable species as well as halogeton.

Conservationists have shown an increasing interest in the vegetation and soils of the salt-desert-shrub type and a desire to improve forage production from Gray Desert soils. Since halogeton has invaded soils of this type, it seemed desirable to determine the effects of halogeton on the chemical and physical characteristics of 3 soils supporting salt-desert-shrub vegetation.

Dye (1956) found that the leaf-seed-sepal fraction of halogeton contained a high percentage of sodium. The highest concentration of oxalate, presumably mostly sodium oxalate, occurred in February. Morton *et al.* (1959) pointed out that halogeton plants accumulate large amounts of sodium and that annual additions of halogeton residues may increase the salinity of the surface soil.

Haas (1957) was probably among the first to recognize that halogeton might influence soil chemical characteristics. He has shown that pH, exchangeable sodium, and soluble salts in the surface soil of 2 vegetation types increased as the weight of halogeton added to the soil was increased. He also indicated that, in general, the density of crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) decreased as the salinity of the soil increased, and the density of halogeton increased as the salinity of the soil increased.

Williams (1959) showed that sodium is essential for maximum growth and development of halogeton in nutrient culture.

Roberts (1950) and Fireman and Hayward (1952) have shown that the salt content and pH of the soil increases progressively from barren areas to beneath shadscale (*Atriplex confertifolia* [Torr. & Frem.] S. Wats.) and greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.). In addition, there were higher pH values under old shrubs and at greater depths than under young shrubs. Roberts pointed out that certain species of plants are able to absorb salts from deep in the soil profile and to concentrate these salts in the surface horizon. Smith and Rauchfuss (1958) reported that aqueous extracts from halogeton had

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[1] The data in this paper were collected as a part of Nevada Agricultural Experiment Station Project U-1, financed in part by the Bureau of Land Management with Salt-Desert-Shrub Research Funds.

[2] Range Conservationist, Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture and Assistant Plant Ecologist, Nevada Agricultural Experiment Station, respectively.

TABLE I. Chemical and physical characteristics of the 3 soils used in the study

Soil	pH	E C x 10^3	Organic matter	Texture % sand	Texture % silt	Texture % clay	⅓ atm percentage	15 atm percentage	Cation exchange capacity (Meq/100g)	Exchangeable cations (Meq/100g) Na	Exchangeable cations (Meq/100g) K	Soluble cations (Meq/100g) Na	Soluble cations (Meq/100g) K	Soluble cations (Meq/100g) Mg	Soluble cations (Meq/100g) Ca
Shadscale	8.1	1.3	0.84	54.7	35.4	9.9	15.0	8.3	13.9	0.78	3.3	0.150	0.054	0.031	0.130
Whitesage	8.1	0.9	1.06	57.3	35.8	6.9	17.1	9.2	13.3	0.28	3.1	0.045	0.042	0.020	0.099
Saltsage	8.1	0.9	0.90	35.6	52.1	12.3	22.8	11.4	29.9	0.33	5.0	0.043	0.066	0.030	0.088

higher pH and conductivity values than the distilled water used to make the extracts.

Little is known about the leaching of chemical constituents from halogeton or about the effects of these constituents on the chemical and physical characteristics of soil. This study attempted to simulate a long-time cumulative toxic process during one year in the greenhouse. Certainly the treatments used would not be equivalent to any in nature in any one year.[3] However, halogeton has been growing on some sites in Nevada for at least 25 yr. Over this period a cumulative toxic effect may become pronounced, since the low annual precipitation would not leach the added salts out of the root zone.

Our treatments were designed to give large differences so that any toxic effect of halogeton would become evident. If a toxic constituent is present, other studies can be designed to give more precise information on the effect of halogeton leachate on soils and plants.

The objectives were as follows: 1) to develop experimental procedures that are useful in leaching studies; 2) to determine the effect of halogeton leachate on the chemical and physical characteristics of 3 Gray Desert soils; and 3) to evaluate the effect of halogeton on soil characteristics under field conditions.

METHODS

The treatment combinations used were 3 levels of halogeton mulch, 3 soils, and 4 leaching periods in a factorial experiment with a randomized block design replicated 3 times.

The surface 5 in. of soil supporting the following 3 vegetation types was used in this study: shadscale, whitesage (*Eurotia lanata* [Pursh] Moq.) and saltsage (*Atriplex nuttallii* S. Wats.). In the text and tables these soils will be referred to as shadscale, whitesage, and saltsage soils, respectively. Halogeton was not growing on these soils at the time of collection. Various chemical and physical characteristics of these 3 soils are shown in Table I. Soil samples were passed through a ¼ in. mesh screen and 1½ lb of air-dry soil were placed in 6 in. clay pots. The pots had been coated inside and out with two layers of clear plastic.

The halogeton was collected in the fall of 1957 near Wells, Nevada. The dry material was ground in a Wiley mill and placed on the surface of the potted soil to depths of one and 3 in., approximately equal to 27,000 and 95,000 lb of air-dry material per acre, respectively. A check treatment was also included.

Four leaching periods (1, 2, 3, and 4 months) were used. Pots were irrigated at intervals to keep water percolating through the halogeton-soil system. The leachate was collected in aluminum dishes and poured back into the pots at weekly intervals. Composite samples of leachate were collected at monthly intervals for pH, conductivity, sodium, and potassium analyses. After each leaching period, the halogeton crust was removed from the soil surface, dried, and ground for sodium analysis.

After completion of the last leaching period all the soil samples were ground to pass through a 2 mm screen. Chemical and physical determinations were made on these samples.

The pH of a saturated paste was obtained by the glass electrode (method 21 b of the U. S. Salinity Laboratory 1954).

Soil salinity was indexed by the electrical conductivity of a saturation extract (methods 3a and 4b of the U. S. Salanity Laboratory 1954).

The organic matter content of the soil was determined by a modified Walkely-Black method, as outlined by the Oregon State College Soil Testing Laboratory (1954).

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[3] Yields of halogeton in 1959 ranged from 800 to 10,000 lb per acre depending upon the site.

Mechanical analyses were made by the Bouyoucos (1951) method as modified by Youngberg (1957).

One-third and 15 atm moisture percentages were determined by the pressure-cooker and pressure-membrane methods, respectively (methods 30 and 31 of the U. S. Salinity Laboratory 1954).

Cation-exchange capacity of the soil was estimated by the Peech *et al*. method (1947) as modified by Bianchi (1959).

Total sodium and potassium were determined by flame photometer analysis of the ammonium acetate leachate from the samples (Bianchi 1959).

Soluble sodium, potassium, calcium, and magnesium were determined by flame photometer analysis of saturation extracts from the samples (methods 3a, 10a, and 11a of the U. S. Salinity Laboratory 1954). Exchangeable cations were determined by difference between total and soluble cations. Sodium content of the halogeton mulch was determined by flame photometer analysis of solution remaining after wet digestion of the mulch material (methods 54a and 57a of the U. S. Salinity Laboratory 1954).

Soil-crust strength was measured by the modulus of rupture technique (Richards 1953).

The percolation of water downward through the treated soil was determined. Eighty-five grams of soil were packed uniformly in extraction tubes. A constant head of water was maintained on moistened samples in the tubes. The volume of water passing through these columns was collected and measured hourly for 4 hr.

The capillary rise of water in the treated soil was also measured. Glass tubing 12 in. in length and 0.48 in. inside diameter was packed uniformly with soil. A cotton plug was placed in one end. These tubes were placed upright in a pan of water and the height of water rise was determined every 2 hr for a 4 hr period. Percolation and capillary rise of water were measured on samples composited from the first and second month samples and from the third and fourth month samples.

Chemical and physical determinations were compared statistically except where composite leachate samples were used. The pH values were converted to hydrogen-ion concentration and electrical conductivity values to concentration (meq/liter) for analysis of variance. Treatment means and interactions were compared by use of Duncan's multiple range test (1955).

After the greenhouse and laboratory phases were completed, it seemed desirable to evaluate changes in the chemical and physical characteristics of the soil which may have been affected by leachate from halogeton residues under field conditions in the salt-desert-shrub type.

The plots selected for this field evaluation were in an exclosure fenced in 1952 and were a portion of another study. Three 100 sq ft circular plots were used. One had been treated with a soil sterilant (Monuron[4]) at the rate of 10 lb per acre, and the other two plots had been treated at the rate of 15 lb per acre. Both applications were made in the summer of 1952. The ground cover at the time of treatment was composed of 12% whitesage and 9% halogeton. In 1953 most of the whitesage on the plots was dead. In 1959 there was only a trace of living whitesage. During 1953-1959 the average yearly cover of halogeton on the plots was approximately 14%, whereas, outside the plots but still within the exclosure, halogeton has been virtually excluded by increased whitesage cover resulting from protection. Average annual air dry yield of halogeton on the treated plots was approximately 250 lb per acre.

These plots, therefore, offer an excellent opportunity for study of soil differences under two sets of vegetative conditions: (1) where halogeton has persisted for 7 growing seasons, and (2) where little or no halogeton was present for 7 growing seasons (Fig. 2).

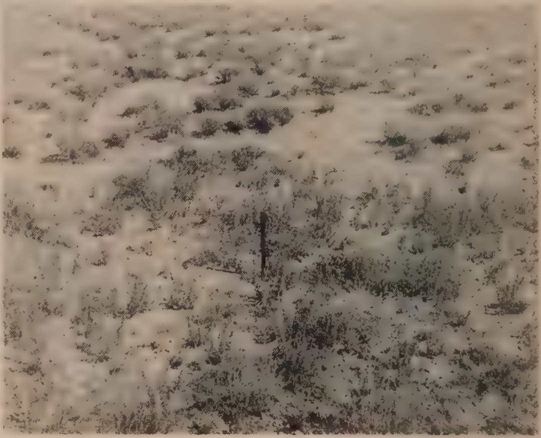

FIG. 2. Plot sprayed with Monuron in 1952. Photograph taken in 1959 shows halogeton on sprayed plot (foreground) and whitesage on the untreated area (background).

Soil samples were taken inside and outside the halogeton plots at one inch intervals to a depth of 4 in. The soil was passed through a 2 mm screen and chemically analyzed for exchangeable and soluble sodium. Physical determinations included modulus of rupture, water percolation, and capil-

[4] Chemically 3-(p-chloropheny) 1, 1 dimethylurea.

lary rise of water. The methods for these analyses have been described above.

RESULTS

Chemical characteristics of halogeton mulch and leachate

A partial chemical analysis of the halogeton mulch and of the leachate is presented in Tables II and III. The halogeton mulch averaged 6.77% sodium before the leaching treatments. Approximately 88% and 52% of the total sodium in the halogeton mulch were removed from the one and 3 in. mulch levels, respectively, by the leaching treatments. Absence of a significant difference among periods of leaching indicated that most of the sodium was extracted during the first month. The tap water used for leaching had a pH of 6.7, a conductivity of < 0.1 mmhos/cm, a sodium content of 0.27 meq/liter, and a potassium content of 0.05 meq/liter. After the first month of leaching the effluent had a pH of 9.3, a conductivity of 29.3 mmhos/cm, a sodium concentration of 279 meq/liter, and a potassium content of 140 meq/liter. Evidently soluble materials were removed from the mulch by percolating water and carried into the soil.

TABLE II. Mean per cent sodium in unleached and leached halogeton mulch[1]

Per cent total sodium in unleached halogeton mulch	6.77
Per cent sodium remaining in leached halogeton mulch:	
In 1 in. mulch	0.81^{a}
In 3 in. mulch	3.27^{b}
Per cent of total sodium removed from halogeton mulch by leaching:	
From 1 in. mulch	88.03^{a}
From 3 in. mulch	51.70^{b}

[1] Any two means with different superscripts are significantly different at the one per cent probability level.

TABLE III. The pH conductivity, and sodium and potassium contents of composite leachate samples collected each month and of tap water

Month	pH	Conductivity (E C x 10^{3})	Sodium (Meq/liter)	Potassium (Meq/liter)	Osmotic pressure (Atm)
1	9.3	29.3	279	140	11.4
2	9.2	25.8	187	123	10.5
3	9.2	18.7	165	15	7.7
4	9.1	35.3	421	49	15.3
Tapwater	6.2	<0.1	0.27	0.05	<0.3

Chemical Characteristics of Soils

Depth of halogeton mulch, soil source, leaching period, and soil x depth of mulch interaction were sources of significant variations in chemical characteristics of soils. In Table IV the means of the soil source and the depth of halogeton mulch treatments are compared. With the exception of pH, soluble potassium, and soluble magnesium there was a significant increase in all chemical constitutents and in electrical conductivity for each added increment of halogeton mulch. The pH values were highest at the zero and 3 in. levels and lowest at the one inch level. Soluble magnesium and potassium were highest at the 3 in. mulch level and lowest at the zero and one inch levels. There were no differences among the shadscale, saltsage, and whitesage soils in pH, electrical conductivity, soluble calcium, or soluble magnesium. At the 5% level of probability, soluble sodium was higher in the saltsage soil than in the whitesage or shadscale. These soils differed significantly in exchangeable sodium, exchangeable potassium, and soluble potassium. These constituents were higher in the saltsage soil than in either the shadscale or whitesage soil. The leaching periods resulted in a significant difference only in the exchangeable sodium constituent. Comparison of treatment means showed exchangeable sodium content of the soil to be significantly lower after 3 months of leaching than after one, two or 4 months. Conductivity and sodium and potassium concentration of the effluent were also lowest after 3 months of leaching (Table III).

The soil x depth of mulch interaction showed significant variation in pH, exchangeable sodium, and soluble sodium (Fig. 3). At the zero and one inch mulch levels pH values were similar in all 3 soils. The shadscale and whitesage soils had higher pH values than the saltsage soil at the 3 in. mulch level. Exchangeable sodium values were similar for all 3 soils at the zero and one inch mulch levels. However, the saltsage soil had approximately 30% more exchangeable sodium at the 3 in. mulch level than the average of the shadscale and whitesage soils at that level. Soluble sodium values followed the same trend as the exchangeable sodium. At the 3 in. mulch level, the saltsage soil contained approximately 45% more soluble sodium than the average of the other two soils.

Physical Characteristics of Soils

Changes in the physical characteristics of the treated soils were evaluated by 3 measurements: modulus of rupture, percolation of water, and capillary rise of water (Table V).

Analysis of variance of modulus of rupture data showed that soil source, depth of halogeton mulch,

TABLE IV. Chemical characteristics of soil as affected by depth of mulch and soil source

Treatment	pH	Conductivity E C x 10^3	EXCHANGEABLE CATIONS (Meq/100g)		SOLUBLE CATIONS (Meq/100g)			
			Sodium	Potassium	Sodium	Potassium	Calcium	Magnesium
Depth of halogeton mulch								
0 in.	8.8^{a1}	1.3^a	0.44^a	3.98^a	0.07^a	0.04^a	0.08^a	0.03^a
1 in.	8.5^b	3.4^b	4.41^b	4.64^b	0.77^b	0.05^a	0.16^b	0.04^a
3 in.	8.8^a	9.8^c	11.48^c	5.84^c	3.40^c	0.14^b	0.91^c	0.11^b
Soil source:								
Shadscale	8.6	4.7	4.61^a	4.37^a	$1.17^{1\,2}$	0.67^a	0.09	0.05
Saltsage	8.8	5.3	6.47^b	6.01^b	1.71^2	0.97^b	0.11	0.07
Whitesage	8.8	5.5	5.26^a	4.08^a	1.36^1	0.73^a	0.14	0.14

[1] Any two means with different alphabetical superscripts are significantly different at the one per cent probability level.
[2] Any two means with different numerical superscripts are significantly different at the 5% probability level.

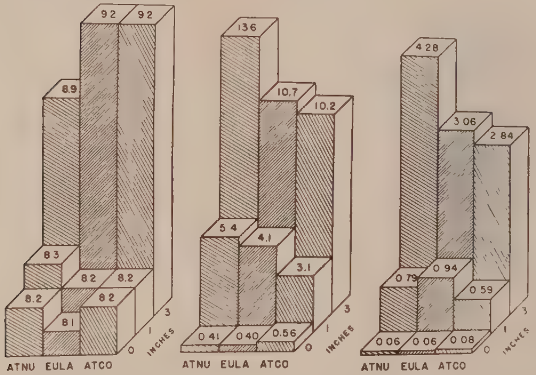

FIG. 3. Effect of depth of halogeton mulch on the pH, exchangeable sodium (meq/100g), and soluble sodium (meq/100g) of saltsage (Atnu), whitesage (Eula), and shadscale (Atco) soils. The 0, 1, and 3 inches refer to the check and depths of halogeton mulch treatments, respectively.

period of leaching, and all first and second order interactions were sources of significant variation.

Crust strength increased with each added increment of halogeton mulch. Saltsage soil formed the hardest crust of the 3 soils tested. Shadscale and whitesage crusts were similar in strength. Soils leached for one month had less crusting tendency than soils leached 2, 3 or 4 months. The 3 month leach period resulted in the greatest crust strength, but not significantly greater than that of the 4 month period. The saltsage soil had greater crust strength at both the one and 3 in. mulch levels than the other 2 soils at those levels. For all leaching periods the crusting tendency of the saltsage soil was greater than for the other two soils. Soil with a 3 in. mulch depth leached for 3 months had the strongest crust.

Analysis of variance of the percolation data showed that soil source, depth of halogeton mulch, leaching period, and all first and second order interactions were sources of significant variation. Water movement through the soil decreased with each added increment of halogeton mulch (Table V). Percolation was most rapid in the whitesage soil and slowest in the saltsage soil. This relationship between the whitesage and saltsage soils existed for all mulch levels and for all periods of leaching. The shadscale soil was intermediate. Percolation was more rapid in the 3 + 4 month composite sample than in the 1 + 2 month sample. Treatment with 3 in. of halogeton mulch reduced percolation in both the 1 + 2 and the 3 + 4 month composite soil samples.

Analysis of variance of the capillary rise data revealed that soil source, depth of halogeton

TABLE V. Physical characteristics of soils as affected by depth of halogeton mulch, soil source and period of leaching

Treatment	Modulus of rupture (Dynes/sq cm)[1]	Percolation (Ml/4 hr)[2]	Capillary rise (Cm/4 hr)[2]
Depth of halogeton mulch:			
0 in.	$62^{a\,3}$	103.17^a	20.02^a
1 in.	130^b	43.28^b	10.01^b
3 in.	310^c	27.83^c	8.09^c
Soil source:			
Shadscale	152^a	53.61^a	12.90^a
Saltsage	194^b	41.33^b	11.20^b
Whitesage	156^a	79.33^c	14.01^c
Period of leaching:			
1 month	148^a	53.04^a	$12.57^{1\,4}$
2 months	170^b		
3 months	180^c	63.15^b	12.90^2
4 months	174^{bc}		

[1] Mean of 6 replications.
[2] Percolation and capillary rise trials were conducted with 1 + 2 month and 3 + 4 month composite samples.
[3] Any two means with different alphabetical superscripts are significantly different at the one per cent probability level.
[4] Any two means with different numerical superscripts are significantly different at the 5% probability level.

mulch, leaching period, and all first and second order interactions except soil source x leaching period were sources of significant variation. Each increment of halogeton mulch resulted in a reduction in height of water rise (Table V). The 3 in. mulch level was most effective in reducing the capillary rise of water in the soils. Capillary rise was greatest in the whitesage soil and least in the saltsage soil. Differences due to leaching periods were significant at the 5% probability level only. At this significance level, the capillary rise of water was greater in the 3 + 4 month composite sample than in the 1 + 2 month composite sample. Water rose to its highest level in the whitesage soil at the zero inch mulch level and to its lowest level in the saltsage soil at the 3 in. mulch level. Treatment with 3 in. of mulch reduced capillary rise most in the 3 + 4 month composite sample.

Field evaluation of soil changes caused by leachate from halogeton residue

Analyses of variance showed that replication (plots), location (inside and outside of treated plots), and depth of sampling were sources of significant variation in chemical and physical characteristics of soils. In Table VI location means are compared.

TABLE VI. Chemical and physical characteristics of soil from inside and outside of plots sterilized in 1952 and supporting halogeton since 1953

Soil characteristic	Location	
	Inside	*Outside*
pH	8.6[a1]	8.2[b]
Conductivity (E C x 10^3)	2.13[a]	0.52[b]
Exchangeable Sodium (Meq/100g)	2.91[a]	0.27[b]
Soluble Sodium (Meq/100g)	0.40[a]	0.02[b]
Modulus of Rupture (Dynes/sq cm)	43.9	38.2
Percolation (Ml/4 hr)	169.5[a]	258.5[b]
Capillary Rise (Cm/4 hr)	25.0[a]	29.2[b]

[1] Any two means with different superscripts are significantly different at the one per cent probability level.

Replication differences (except for exchangeable sodium) were due to differences in the cover of halogeton on the plots for the past 7 yr. Electrical conductivity, pH, exchangeable sodium, and soluble sodium were significantly higher inside the plots supporting halogeton than outside where no halogeton exists. There were no significant differences in crusting tendency between the inside and outside, although the trend is for a stronger crust on the halogeton plots. Percolation and capillary rise of water were both significantly lower inside the halogeton plot than outside.

These results showed that, under field conditions, precipitation did leach chemical constituents from halogeton residue and that these constituents were deposited in the soil. With time, therefore, the trend is for the soil environment to become unfavorable for plant growth for reasons to be discussed.

The results also showed that, in general, inside the halogeton plots pH, conductivity, exchangeable sodium, and soluble sodium values were higher in the surface 3 in. of soil than at a depth of 4 in. Crusting tended to be greater and percolation less in the surface inch of soil than at the lower depths, although differences due to depth were not significant. Capillary rise of water was significantly less in the surface two inches of soil than at the lower depths.

The data illustrate that changes in the chemical and physical characteristics of the soil due to leachate from halogeton residue were manifested principally in the soil surface where seeds are planted and where germination occurs. In addition, normal precipitation did not leach the chemical constituents out of the root zones. Even though the soil changes described would not affect the growth of even salt-sensitive plants, the data show a definite tendency for these soil changes to be cumulative.

DISCUSSION

The results of the greenhouse, laboratory, and field portions of this study revealed that leachate from increasing increments of halogeton mulch increased the values of pH, electrical conductivity, exchangeable sodium and potassium, soluble sodium, potassium, calcium, and magnesium, modulus of rupture, and decreased percolation of water, and capillary rise of water.

Chemical changes in soil were the direct effects of the salts leached from the halogeton mulch. Alterations of physical properties of the soil were the indirect effects of these salts (Ratner 1935, Kotzmann 1935, Cassidy 1944, Reeve *et al.* 1954, and Brooks *et al.* 1956). These workers reported that the magnitude and rate of change of physical alterations were greater in sodium treated soils than in potassium treated ones. From these studies and from the chemical analyses of halogeton mulch and the effluent in in this study, obviously the changes in the soil environment described in this experiment were due principally to sodium.

These changes in the soil environment have many implications with respect to soils in the salt-desert-shrub type now supporting or capable of supporting halogeton. The discussion will point out ways in which halogeton may, given enough time, have adverse effects on soils and plants.

Halogeton has approximately the same effect on soil as do greasewood and shadscale. These shrubs grow widely spaced and the salt content decreases progressively from beneath the plants to barren areas (Roberts 1950, Fireman and Hayward 1952). Other soil properties associated with lower salt content may be prevalent in the bare areas between the shrubs. In such areas conditions would be more favorable for plant growth than beneath the shrubs. Halogeton, however, grows in dense stands in which most of the soil surface would be affected by water percolating through the halogeton litter. In such instances, once halogeton has altered the soil a closed community exists and natural or artificial revegetation of such areas is complicated by the following phenomena.

Leachate from halogeton carries soluble salts into the soil. Ayers and Campbell (1951) pointed out that the amount of soil moisture available between field capacity and a 15 atm tension decreased as the salinity of the soil solution increased. The high soil moisture tensions generally associated with the salt-desert environment may be aggravated by an increase in osmotic pressure due to increased soil salts. For example, the osmotic pressure of the soil solution due to addition of 3 in. of halogeton mulch was 3.5 atm. The resulting total soil moisture stress may be enough to decrease production of existing species or to reduce the germination of native or introduced species.

Ravikovitch and Muransky (1958) found that high salt concentrations inhibited the activity of microorganisms which break down organic residues. Nitrification also decreased as soil salinity increased. Since soils of the salt-desert type are deficient in nitrogen, any blockage of the nitrogen cycle tends to decrease plant growth.

Total soluble salts may restrict the availability of moisture to plants and reduce nitrification, and in addition certain salts may injure or depress the growth of specific plants. Ratner (1935) found that if the exchange complex becomes more than 40-50% sodium saturated, nutritional disturbances may result. In general, with increasing exchangeable sodium percentage, the accumulation of potassium, calcium, and magnesium in the plant decreased (Bower and Wadleigh 1949). In this or a similar manner, the sodium from halogeton may have a direct toxic effect on some plants.

Sodium in the soil may also exert important indirect effects on plant growth through adverse changes in the physical properties of soils. The U. S. Salinity Staff (1954) pointed out that saline soils generally have unstable aggregates. Soils with low stability of structure slake when wetted and may develop a hard surface crust when dry. Some factors favoring crust formation are high exchangeable sodium, low organic matter, and puddling. Results from modulus of rupture measurements showed that soils treated with halogeton mulch form much harder crusts than the untreated soils. These crusts can be a serious barrier to the emergence of seedlings. In addition, any type of tillage on halogeton-infested salt-desert soils may lead to a serious crusting problem.

As the exchangeable sodium content increases the soil deflocculates or disperses. With increased dispersion the percolation of water becomes slower. Measurement of percolation showed that halogeton was effective in reducing total water flow and the rate of percolation. Slow percolation would increase the amount of overland flow from summer cloudbursts and cause an erosion hazard. This runoff problem would also be aggravated by a hard impermeable crust. Water lost by runoff would be unavailable for plant growth.

Crusts and slow percolation would decrease the amount of moisture added to the soil by summer storms, and a reduced rate of capillary movement of water would influence the distribution and availability of moisture within the soil mass. Treatment with halogeton mulch reduces the total capillary rise of water and the rate of rise. These could be important factors in the germination of seeds and early development of seedlings since water lost from the surface 6 in. of soil by evaporation could not be replaced by capillarity if the soils had been altered by salts leached from halogeton.

Of the 3 soils used in this study, the saltsage soil was altered most seriously by treatment with halogeton mulch. From the standpoint of range conservation, pronounced alteration of saltsage soil is important since this species is a palatable and nutritious forage. This saltsage soil had a finer texture than that of the shadscale or the whitesage soil. Associated with finer texture is a higher base-exchange capacity (Table I); therefore more sodium from halogeton mulch can be adsorbed and retained by the soil colloids. In addition, soluble salts would leach out of the surface soil more slowly because the rate of water percolation in a saltsage soil is slower than in either the shadscale or the whitesage soils. Also, the surface crust formed from a saltsage soil is harder than crusts from the other two soils. These 3 factors would make a halogeton infested saltsage soil less favorable for natural or artificial revegetation than either a shadscale or a whitesage soil.

The effects of halogeton invasion of either saltsage or shadscale areas is complicated by the large amounts of soluble salts in extracts from the saltsage and shadscale plants themselves. Water extracts from these two plants had electrical conductivity values of 10 and 15 mmhos/cm, equal to concentrations of approximately 120 and 190 meq/liter or osmotic pressures of 4.8 and 5.9 atm, respectively. Leachates from the litter of these shrubs, together with leachate from halogeton, can add appreciable amounts of soluble salts to the soil surface. Since halogeton frequently grows in the bare spaces between the shrubs, the total soil surface area is subjected to additions of soluble salts. This phenomenon would not be as pronounced in the whitesage type since the conductivity of whitesage extract is only 2.9 mmhos/cm, equal to a concentration of 3.1 meq/liter or osmotic pressure of 1.0 atm.

SUMMARY

A study was undertaken to determine whether leachate from halogeton residue can alter the chemical and physical characteristics of the soils of the salt-desert-shrub type. Greenhouse, laboratory, and field evaluations were made by using standard analytical and statistical procedures.

The results showed that chemical constituents, principally sodium, are leached from halogeton mulch and are deposited in the soil. Electrical conductivity, exchangeable sodium and potassium, and soluble sodium and calcium in the soil increased significantly with each added increment of halogeton mulch. After treatment, soil from the saltsage vegetation type contained more exchangeable and soluble sodium than the soil from the shadscale and whitesage vegetation types.

Results of physical measurements revealed that crusting tendency of all soils increased and percolation of water and capillary rise of water decreased with each added increment of halogeton mulch. The physical characteristics of the saltsage soil were altered most seriously by the treatments.

Results of the field evaluation showed that pH, electrical conductivity, exchangeable sodium, and soluble sodium were higher in the soil on plots supporting halogeton for 7 yr than immediately outside the plots where there was no halogeton. Percolation of water was slower, and capillary rise of water was less inside the halogeton plots than outside. Inside the plots, the adverse effects were manifested principally in the surface soil.

Alteration of the chemical and physical properties of the soil can effect plant-soil relations in the following ways: increased soluble salts, increased osmotic pressure, blockage of the nitrogen cycle, specific ion effect, crusting, reduced percolation and capillary rise of water, runoff, and erosion.

The soil changes that have taken place under field conditions over a 7 yr period are not severe enough to limit plant growth. However, field and laboratory results revealed a definite tendency for adverse soil effects to become cumulative.

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RESPONSES OF TWO SUBSPECIES OF ORCHARDGRASS (*DACTYLIS GLOMERATA* SUBSP. *LUSITANICA* AND *JUDAICA*) TO INCREASING SOIL MOISTURE STRESS[1]

Cyrus M. McKell, Eugene R. Perrier, and G. Ledyard Stebbins[2]

Introduction

Growth responses of plants in relation to soil moisture stress have received considerable investigation. However, with the exception of corn, very little soil moisture stress research has been done with members of the *Gramineae*, a group of plants with a wide range of ecological adaptations to deficient soil moisture. Adaptation within the broad spectrum of soil moisture stress conditions may be expressed in various ways: perennial desert grasses produce only limited growth or go into dormancy during dry periods, annual grasses complete their life cycle during a moist period, perennial grasses grow only in summer in arctic or alpine habitats, perennial grasses may grow almost continuously in cool maritime habitats, and grasses limited to warm moist tropical and sub-tropical habitats may have periods of reduced growth during seasonal droughts. Most environments where grasses grow have a period of drought. As a result grasses, particularly perennial species, since they persist through dry periods, might be expected to be sensitive to changes in soil moisture conditions.

Grasses have certain characteristics important in soil moisture stress studies. Their leaves undergo large amounts of elongation and their intercalary meristem is in a protected location. The well-ramified fibrous root system is very efficient in extracting moisture from the soil. A large number of grass species variously adapted to xeric or mesic environments is available for experimentation.

In their review article, Richards and Wadleigh (1952) mentioned that "There is little direct information bearing on the relation of plant growth to soil-moisture stress. Nonetheless, recent information of both direct and indirect nature indicates that the vegetative growth of some plants decreases significantly as the soil moisture stress increases in the 1-atm range and becomes zero before a soil moisture stress of 15 atm is obtained." Studies that would serve as a basis for this statement include those of Wadleigh and Gauch (1948), who found that leaves of cotton ceased to elongate when soil moisture stress reached 12-14 atm. Blair, Richards and Campbell (1950) measured the rate of stem elongation of sunflower in relation to soil moisture depletion and found a decrease in the elongation rate before half of the "available water" was used. Stem elongation ceased before the permanent wilting point was reached. Haynes (1948) studied the effect of moisture availability on the growth of corn in containers in the greenhouse. The maximum soil moisture tensions before irrigation were 0.01, 0.7 and 12.0 atm and the corresponding vegetative growth in grams of dry weight per plant was 33.9

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24.0 and 11.8, respectively. Salter (1954) observed a reduction in the vegetative growth of tomatoes when soil moisture tensions exceeded 0.7 atm (10 cm Hg) before rewatering.

Many of the factors affecting soil moisture—plant growth relations were discussed by Hagan (1955). Several examples were cited to show that some plant responses occur before all available moisture is depleted under certain conditions. Included in Hagan's review were 2 check lists of conditions which would, or would not, raise the probability that crop yields could be increased by irrigations at low soil moisture stress.

Stanhill (1957) reviewed results from 80 soil-moisture-regime experiments. In over 80% of the studies, growth was affected in a negative manner by differences in the amount of available water depleted before the soil was rewetted. Annual plants showed a greater response to deficient soil moisture than did perennial plants possibly because many annuals are grown for their vegetative tissue while most perennials studied are grown for their reproductive organs.

Slatyer (1957) stated in his review that many vital physiological proceses including cell enlargement, photosynthesis, and growth are affected by soil moisture stresses occurring before the permanent wilting point is reached. Such plant processes are affected by decreased turgor pressure, decreasing hydration, and a combination of tissue hydration and stomatal closure, respectively.

The bulk of experimental results supports Slatyer's conclusions. Disagreement with the often cited dictum (Veihmeyer and Hendrickson 1927, Veihmeyer 1956) that water is equally available to plants between field capacity and the permanent wilting point is more apparent than real inasmuch as plant properties other than vegetative growth were measured and most experiments were with perennial species grown under field conditions.

This study compares the responses of two subspecies of orchardgrass (*Dactylis glomerata* L. subsp. *lusitanica* and *judaica* Stebbins & Zohary) that are dissimilar in their ecological adaptation to soil moisture conditions but are closely related genetically. The study was designed to measure moisture use, leaf elongation, production of leaf tissue and response to clipping intensity under conditions of increasing soil moisture stress.

Description of Plant Species Studied

The two orchardgrass subspecies studied were described by Stebbins and Zohary (1959). They differ ecologically and morphologically (Fig. 1) but are interfertile genetically. The two subspecies have separate distribution patterns.

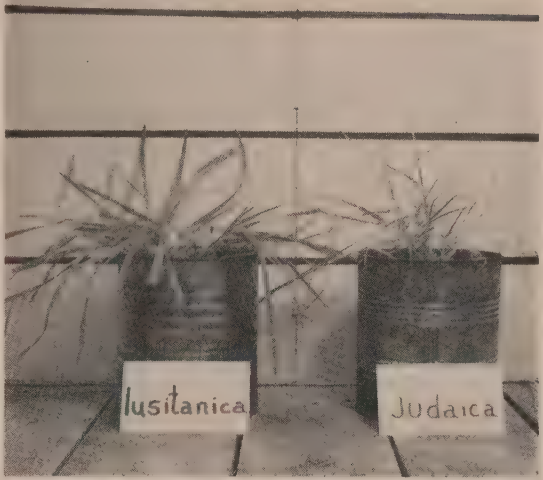

Fig. 1. Plants of *Dactylis glomerata* subsp. *lusitanica* and *judaica* growing in No. 10 cans in preparation for soil moisture stress study.

Subspecies *lusitanica* is known from the coastal area of central Portugal and is characterized by its vigorous growth, deep green foliage, leaves 6-12 mm wide, stout culms, long ligules with a green midrib, and densely contracted panicles. Reports indicate that habitat conditions are variable within the mild coastal climate of western Portugal, where *lusitanica* is found. The plant does not characteristically go into a summer dormancy. Plants of *lusitanica* in northern California are vigorous and remain green throughout the year when sufficient moisture is available.

Subspecies *judaica* is known at present from Israel, but its occurrence in regions to the north and east of Israel is not unlikely. Plants of *judaica* are glaucous and have leaves 4-6 mm wide and contracted panicles on the summit of slender culms. Leaves are less firm than those of *lusitanica*. *Judaica* has been collected in its native habitat on rocky limestone slopes where it grows in association with the shrubby *Poterium spinosum* L. Subspecies *judaica* is a plant typical of a dry Mediterranean climate. In northern California it grows in winter, flowers in late April and early May, and goes dormant in the summer.

A difference in moisture content of leaf tissue was noted in a preliminary study of the two subspecies. Under comparable conditions of soil moisture, leaf tissue of *lusitanica* had an average moisture content of 83.5% as compared with that of *judaica* which was 77.7%.

Survival of 20 clonal divisions of each subspecies set out in January, 1957, at two locations in California indicates to a limited extent the ecological adaptation of each subspecies to arid conditions. At Hopland Field Station in the chaparral type of north coastal California on cultivated Sutherlin clay loam (mean annual precipitation 35 in.), 75% of the *lusitanica* plants and 45% of the *judaica* plants survived the first year after planting. In comparison, plant survival the first year after planting at the Lowrey Ranch in the dry foothills of the Sacramento Valley on unfertile hardpan clay terrace soil (mean annual precipitation 20 in.) was *lusitanica* 0% and *judaica* 45%.

Procedure

Red bluff sandy clay was used in the study because the clay in this soil is prinicipally of the kaolin type, which is low in expansion and contraction characteristics. The soil had a mean bulk density of 1.23 when packed in the experimental cans, a base-exchange capacity of 4.95, a pH of 5.2, and a conductivity of 0.59 x 10^3 mmhos. at 25°C for the saturated extract.

Soil moisture stress was measured by frequent readings of gypsum electrical resistance plugs[3] installed midway in No. 10 cans (1 gal) filled with soil. A calibration curve for the gypsum plugs relating ohms resistance to bars of soil moisture suction (1 bar = .987 atm) was prepared (Fig. 2) from laboratory and field data using a Beckman soil moisture ohmmeter, Model 300, and pressure membrane and porous plate apparatus (Richards 1947, 1948). Several soil samples were taken concurrently with block readings to compare with the calibration curve. Good agreement was obtained.

Forty-two cans of soil with holes punched in the sides near the bottom were each seeded with 8 seeds of *lusitanica* and an additional 42 cans were each seeded with 8 seeds of *judaica*. The number of plants per can was reduced to two after 3 weeks. A randomized-block experimental design was used with 6 replications of the two species reaching 7 moisture stresses (2,8,12,16,20,25 and 28 bars of soil moisture suction).

After 3 months of growth under favorable moisture conditions in the greenhouse all plants were clipped to within one inch of the soil surface and placed in a plant growth cabinet where conditions were held at 18 ± 1°C, relative humidity of 45 ± 5%, a day length of 14 hr, and a light intensity at plant height of 1300 ft-c. Growth chamber conditions were selected to provide a propitious environment which could be repeated. No attempt was made to duplicate the natural environment of either subspecies. Plants were grown for a one month conditioning period in the growth chamber environment, and were then reclipped to the one-inch length, irrigated, and the observational period was begun.

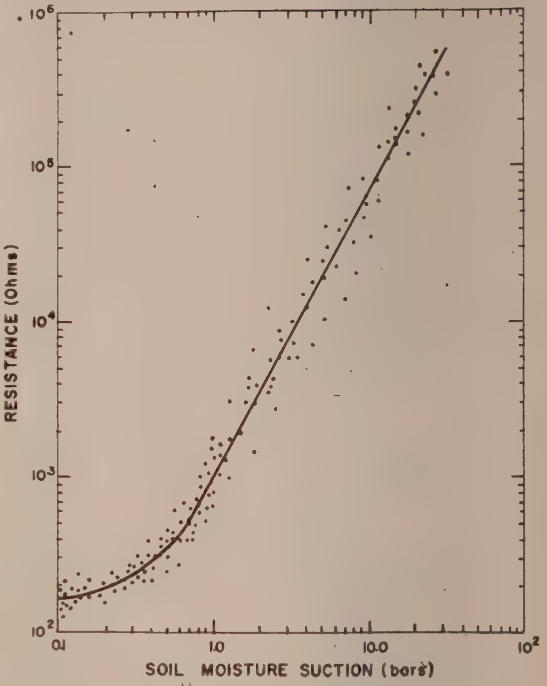

FIG. 2. Calibration curve for concentric electrode gypsum plug.

Moisture readings were made twice or more daily to determine the time required to reach a designated soil moisture stress. Leaf blade elongation was also measured daily using a large headed nail imbedded in the soil adjacent to a particular leaf in a young tiller as a reference point. As a specified moisture level was reached in each designated can the time was recorded and the plants were clipped back to the one-inch level. Clippings were dried at 60°C for 48 hr and weighed on an analytical balance.

As soon as plants in each can were clipped, they were irrigated to maintain favorable moisture conditions for plant growth in preparation for further study.

One month after completion of the first study a second one was initiated. All plants were clipped back to the original one inch length, which was evident by the old leaf sheaths, and 35 cans of each subspecies were selected. Seven replications of 5 clipping frequencies (3 days, 5 days, 7 days, 14 days, and a final clip only) of each subspecies were compared in a randomized-block design.

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[3] A concentric electrode electrical resistance plug manufactured by W. R. Ames Co., Milpitas, California. (The mention of a specific instrument or company is made for identification and does not imply endorsement by the U. S. Department of Agriculture over others of similar nature not mentioned).

Cans were irrigated to saturation initially and no additional water was added during the experiment. Leaf tissue removed after each clipping was oven-dried and weighed on an analytical balance. The gypsum plugs were read to determine the soil moisture stress at each clipping time.

Results and Discussion

The actual moisture stress values reached were close to the expected stress values planned at the beginning of the study (Table I). All observed values, however, were slightly in excess of the planned soil moisture stress values. Considering the rapid change in soil moisture suction that may occur during a short period of active plant growth there is relatively close agreement between the soil moisture suction values of the experimental design and the obtained values.

Table I. Proposed soil moisture suction treatments, mean values actually attained, and leaf weight at time of harvest of each subspecies of orchardgrass

Subspecies	Proposed treatments (bars)	Actual Values (bars)	Leaf weight of grass (grams)
judaica	2	3.6±0.9	0.231±0.014
	8	8.7±0.7	0.341±0.076
	12	14.3±0.3	0.338±0.021
	16	18.2±0.3	0.253±0.101
	20	20.8±0.2	0.306±0.066
	24	25.6±0.3	0.309±0.026
	28	30.4±0.5	0.314±0.019
lusitanica	2	2.6±0.6	0.403±0.016
	8	9.2±0.7	0.475±0.024
	12	12.8±0.4	0.558±0.046
	16	17.4±0.4	0.464±0.054
	20	21.4±0.5	0.478±0.083
	24	26.4±0.7	0.581±0.107
	28	30.6±0.7	0.592±0.024

Soil moisture was used more rapidly by *lusitanica* than by *judaica* between approximately 0.1 and 20 bars of soil moisture suction (Fig. 3). After reaching 20 bars a nearly parallel rate of soil moisture use by the two subspecies prevailed. Subspecies *lusitanica* reached 30 bars of soil moisture suction, which appeared to be a zero rate of moisture use, at 800 hr. Subspecies *judaica* with a lower rate of moisture use did not reach 30 bars until 1000 hr. The greater rate of moisture use by *lusitanica*, as compared with that of *judaica* might be attributed to distinctive morphological features such as its larger leaf area and more open leaf blade. The uniform and relatively slow rate of moisture depletion by *judaica* suggests an ecological adaptation to a xeric habitat. Such an adaptation is reflected in the plant's morphology, typified by the narrow V-shaped leaf blades. However, differences in water use are not unexpected, for Keller (1953) showed them to exist among selected genotypes of commercial orchardgrass.

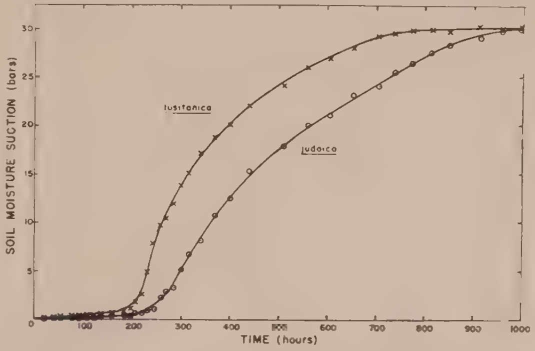

Fig. 3. Rate of water use by *Dactylis glomerata* subspecies *judaica* and *lusitanica*.

A study of the influence of increasing soil moisture stress on leaf-blade elongation revealed that elongation was reduced soon after soil moisture stress began (Fig. 4). A high rate of elongation prevailed when soil moisture suction was below one bar, but elongation was reduced when one bar was exceeded. Little leaf elongation of either subspecies occurred after soil moisture stress reached 3 bars, and it essentially ceased as 5 bars was exceeded. Subspecies *judaica* had the highest rate of elongation. It also had a greater cumulative mean leaf-blade length during the experimental period. However, *judaica* had a longer period of time for growth at low soil moisture

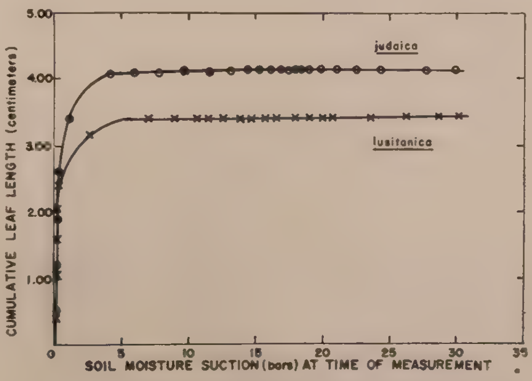

Fig. 4. Cumulative leaf-blade elongation of *Dactylis glomerata* subspecies *judaica* and *lusitanica* as a function of increasing soil moisture stress.

stresses since it was slower than *lusitanica* to reach the higher soil moisture suction values.

Even though leaf-blade elongation ceased as soil moisture stress approached 5 bars of soil moisture suction the plants did not appear wilted. Symptoms of wilting such as rolling, flaccidity, and drooping of the leaf blades did not occur until soil moisture stress reached the 15 bar range.

Although the two orchardgrass subspecies differ ecologically and morphologically they show strikingly similar responses to soil moisture stress in essentially ceasing leaf-blade elongation at about the same soil moisture stress.

Statistical analysis of leaf tissue data indicated no significant difference in leaf tissue produced by subspecies at the various soil moisture values. Such results may mean that the higher soil moisture stresses to which plants were subjected after the first clipping at approximately 2 bars inhibited any significant increases in leaf-tissue production. Several trends in plant response to increasing soil moisture stress appear when the data are presented in graphical form (Fig. 5). Subspecies *lusitanica* appeared to produce a small amount of leaf tissue which consisted mainly of growth of young tillers at the base of the plants. In comparison, *judaica* essentially ceased further growth at soil moisture stresses higher than 5 bars. In its native xeric habitat *judaica* characteristically goes into a summer dormancy as soil moisture diminishes. Field observations of *lusitanica* in several California locations indicate that it does not have a pronounced adaptation for summer dormancy. The cessation of leaf-tissue production by *judaica* at approximately 5 bars and the limited leaf-weight increase by *lusitanica* beyond 5 bars of soil moisture suction is a reflection of the adaptation of these two orchardgrass subspecies to habitats with and without a period of severe soil moisture stress, respectively.

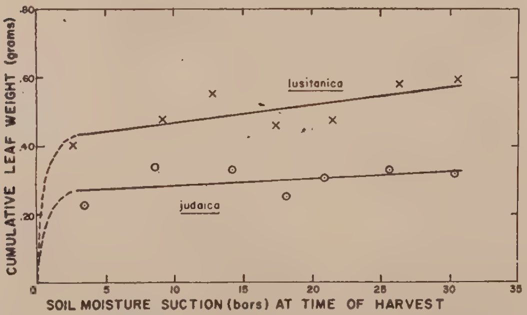

FIG. 5. Cumulative leaf-weight increase as a function of increasing soil moisture as measured at time of clipping.

The total amount of growth, in terms of clipped weight, produced by *lusitanica* was significantly greater than that of *judaica*. Such a difference is not unexpected, however, because *lusitanica* is a more robust plant and normally produces a greater amount of top growth than does *judaica*.

A comparison of elongation and leaf-tissue production in relation to increasing soil moisture stress indicates that elongation ceases before leaf-tissue production is reduced. This result supports the statement by Slatyer (1957, p. 595) that "The effects of water stress on elongation generally act directly through the effect of turgor pressure in cell enlargement." Inasmuch as a large proportion of blade elongation results from cell elongation, one of the first effects of soil moisture stress would be to reduce water available for maintaining cell turgidity and to curtail cell enlargement.

In the second study plant response to clipping frequency in relation to increasing soil moisture stress indicated that the production of leaf tissue ceased at about the same soil moisture stress regardless of clipping frequency (Fig. 6). This corresponds to the results obtained in the earlier study (Fig. 4)." Even though clipping removed some leaf tissue, which would slow down the rate of moisture loss, the curves for cumulative weight increase level off at about the same soil moisture stress for both subspecies and all clipping frequencies. A statistical analysis of the cumulative weights from each clipping frequency at the end of 30 days (Fig. 7) revealed that a clipping interval of 3 days results in a significantly smaller cumulative leaf weight of *lusitanica* than did other clipping intervals. In comparison, no significant differences in weight of leaf tissue of *judaica* resulted from the various clipping frequencies, although the 3 day clipping interval appeared to permit production of the greatest leaf weight. Significantly more leaf tissue was produced by *lusitanica* than by *judaica*.

Several points of interest develop from these results. The first is that different rates of water use may be observed in two genetically related but ecologically and morphologically diverse grasses. A second point is that leaf-blade elongation is considerably influenced by increasing soil moisture stress and leaf elongation may be insignificant when soil moisture stress exceeds 3-5 bars. Even though plants such as *judaica* may be adapted to xeric habitats, leaf-blade elongation ceases at approximately the same soil moisture stress which causes leaf-blade elongation to stop in a plant like *lusitanica* from a mesic habitat. Plants with greater diversity in physiology than the two or-

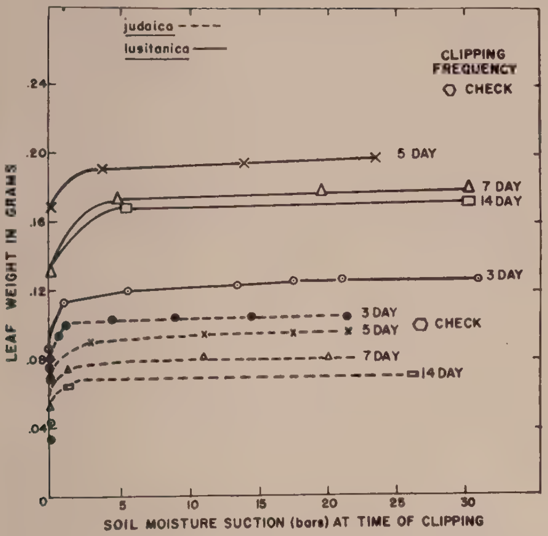

Fig. 6. Cumulative leaf-weight increase as influenced by clipping frequency and increasing soil moisture stress.

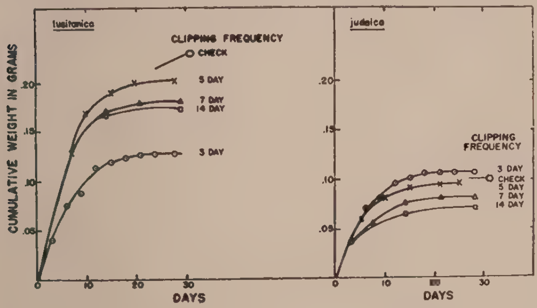

Fig. 7. Cumulative leaf-weight as influenced by clipping frequency and increasing soil moisture stress over a 30 day period.

chardgrass subspecies could respond differently to the soil moisture stresses indicated in this paper. The third point is that production of leaf tissue may be critically reduced by soil moisture stresses that occur before the wilting point is reached. With grasses able to go into dormancy, the dormancy response is difficult to separate from a soil moisture stress response. A fourth point is that the production of leaf weight ceases at about the same soil moisture stress even at different clipping frequencies which perhaps simulate field-grazing conditions.

These results suggest several areas of future research. Information is needed about the relation of increasing soil moisture stress to cell division, cell elongation, cell turgidity, and other growth processes in the intact plant. A better understanding of plant adaptation to environments with a period of soil moisture stress would be possible if more information were available concerning soil moisture depletion patterns and plant growth in various (defined) ecosystems.

In conclusion, although the two grasses may be taxonomic kin and genetically interfertile, but with morphological and ecological differences, the studies reported show that these grasses are very similar in their overall response to soil moisture stress.

Summary

Two ecologically differing subspecies of orchardgrass (*Dactylis glomerata* subsp. *lusitanica* and *judaica*) were studied under the same environmental conditions with respect to their response to increasing soil moisture stress. Subspecies *lusitanica,* native to a mesic habitat in central, coastal Portugal, was compared with subspecies *judaica,* native of a xeric habitat in Israel.

The rate of moisture use was greater by *lusitanica* than *judaica.* Leaf-blade elongation of both subspecies ceased as soil moisture stress exceeded 3-5 bars of soil moisture suction. Subspecies *lusitanica* produced a limited amount of leaf tissue at soil moisture stresses greater than 5 bars. In comparison, subspecies *judaica* did not produce any further increase in leaf weight when soil moisture stress exceeded 5 bars.

As soil moisture stress increased, a clipping frequency of 3 days resulted in a reduction of cumulative leaf weight of *lusitanica.* Subspecies *judaica* did not show any differential response in cumulative leaf weight as a result of various clipping frequencies.

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NOTES AND COMMENT

A PRELIMINARY SURVEY OF EARTHWORMS OF THE TULLY FOREST IN CENTRAL NEW YORK

Most of the hundreds of articles written about earthworms emphasize their economic or biologic importance in one way or another. Their broad classification is well established, some of the life histories are known, and much has been written about their numbers and distribution. We now need detailed ecological studies to determine their real significance in the physical, chemical and biological complex of the soil.

Earthworms are the largest element of the soil fauna, constituting 20 to 80% of its total weight. Bornebusch (1930-31) gives figures showing that the weight of earthworms varies from 95 to 1784 pounds per acre in the soils of Denmark. No weights were taken during this study and no direct comparisons can be made with conditions in Denmark. The numbers collected from the top 6 inches of soil on the Tully Forest showed a wide range of weights and are proof that even their dead bodies contribute a large amount of organic matter to soil. Their biological significance is, however, far greater than their value as fertilizer. Aristotle is said to have called them "The intestines of the earth," and Darwin (1886, p. 813) said, "It may be doubted whether there are many other animals which have played as important a part in the history of the world as have these lowly creatures."

This statement of Darwin may seem exaggerated until we realize that the productivity of the soil determines the plant and animal foods for mankind. Larsen (1956, p. 19) points out that our initial belief that differences in soil were to be explained by the science of geology, that one soil differed from another because of differences in the rocks and sand of which it is composed, has been considerably modified. He says further that plants build soil, and that different plant types build different soil types. Even this statement fails to recognize the important effects of the soil fauna, including earthworms. We are beginning to realize that all of the elements of geology, biology, physiography, and climate interact to determine the kind of soil and what and how much it will produce.

THE TULLY FOREST

The Tully Forest is an area of approximately 2000 acres situated about 25 miles south of Syracuse in Cortland County, New York. The general topography is rolling with rounded ridges and U-shaped valleys running generally north and south. The elevation varies from 1380 to 2020 feet above mean sea level. The soils are mostly thin (less than 6 feet) and underlain with shale or sandstone. In certain areas the shale comes almost to the surface and in several such places a heavy moss carpet has developed. Most of the area formerly was used for agriculture but later abandoned because of low fertility, thin soil, topography, or a combination of these.

About one-third of the area consists of transition types varying from recent agricultural fields to brush-grown areas; one-third of conifer plantations of various ages and species composition; and one-third of hardwood forest which varies considerably in species composition, and in age from pole stage to mature sugar bush and beech stands.

Many soil faunal habitats are furnished by these cover types and still more have been created by 3 artificial ponds which were established 5 years ago.

PURPOSE OF STUDY

This study was carried out to accomplish the following:

1. To determine what species of earthworms are present on the Tully Forest.
2. To determine their distribution and relative numbers.
3. To determine their association with various forest types on the Tully Forest.
4. To secure basic information for more advanced work on the ecology of the soil fauna.

METHODS

Samples were collected during the summer of 1955 from the following forest types:

Old field
Northern hardwoods
White pine plantations
Red pine plantations
Scotch pine plantations
White cedar plantations
Norway spruce plantations

Most of the collections were made during June, July, and August. Earthworms were found in all of these types except the Norway spruce. In addition, they were collected from more restricted locations such as creek banks, shores of ponds, beneath loose bark, under stone walls, and other quite generally distributed but special habitats.

All samples to be counted within a forest type were located at least 50 feet inside the boundary of that type to avoid edge effect. The standard sample of soil for qualitative and quantitative information was 2 feet square and 6 inches deep. For each sample, the soil was removed and shaken through a ¼″-mesh sieve to expose all earthworms. The samples were distributed at random within the type. Three samples were always taken in each type to make the results more representative. However, when no earthworms were found in 3 samples, others were selected in an attempt to locate worms. Such samples were not taken at random but were intentionally located in areas that seemed most favorable.

Collections for qualitative information only were taken in other habitats without respect to the size of the samples.

All specimens were identified as closely as possible from external characteristics and then sent to Dr. Guy Murchie at Flint College, University of Michigan, Flint, Michigan. He is a competent taxonomist in this group and he made the final taxonomic determinations.

RESULTS

Soils

Soil characteristics are very important in determining the distribution of earthworms. The purposes of this study have been set forth and are general in nature. The following generalized treatment of soils therefore is considered adequate for this first investigation.

The soils of this region are classified under the broad category of gray-brown podzolic (forest) soils (Marbut 1935). The soils of the Tully Forest were derived from glacial till. The major soil association found on the forest is the Lordstown-Volusia (Cline 1955). The Lordstown soil is usually characteristic of the steeper slopes and, typically, is shallow, well drained, has a low lime content and lacks a fragipan. The Volusia soil is found on the gently to strongly sloping hills. Here the soil is somewhat poorly drained, the lime content is very low and it also lacks a fragipan.

The texture of the soil was determined in 5 of the types using the Bouyoucos hydrometer method with the following results.

Type	*Sand*	*Silt*	*Clay*
White cedar	18.8	42.0	39.2
Norway spruce	18.4	34.4	47.2
Red pine	20.0	40.8	39.2
Northern hardwood	40.0	41.2	18.8
Old field	32.4	38.4	29.2

The texture of the soil in the white pine plantation was similar to that in the red pine area, and in the Scotch pine the soil was similar to the old field area.

Soil acidity was measured with a Beckman pH meter and was surprisingly constant in the various habitats, not varying sufficiently to account for the presence or absence of the various species of earthworms. The range extended from 4.1 in white cedar to 5.8 in old fields:

White cedar	4.1
Norway spruce	4.7
White pine	4.7
Red pine	4.7
Scotch pine	4.8
Northern hardwood	4.9
Old field	5.8

This relatively low pH places all of the areas on the Tully Forest in an unfavorable category for earthworms according to Murchie (1954) who found that as acidity increases beyond a pH of 6.0 the numbers of species decline. On the other hand Reynolds (1935) checked the occurrence of various species of earthworms with respect to the pH of the soil in sandy coniferous plantations in New York State and found the greatest numbers of species and individuals where the soil had a pH between 5.5 and 4.1. This was also true in this investigation. I believe Murchie's statement indicates that the earthworm populations were lower on the Tully Forest than they would be on deeper, richer, less acid soils.

The moisture content varied from 69% to 7% of the wet weight. All samples were not tested. However, I believe both extremes were measured.

The organic content of the soil was determined with the loss on ignition method (Wilde and Voight 1959). Thirty cores were taken at random through each type. These were thoroughly mixed and 3 samples were then processed for each collection. The results were as follows:

White cedar	18%
Norway spruce	10%
White pine	17%
Red pine	10%
Scotch pine	10%
Old field	10%
Northern hardwood	16%

Earthworm Species Found

Ten species of earthworms, belonging to 7 genera, were found, and more intensive work should reveal a few additional species. These would be more limited in distribution and probably of less general importance. The species found are as follows:

Lumbricus terrestris Linnaeus
Lumbricus rubellus Hoffmeister
Lumbricus castaneus (Savigny)
Allolobophora calignosa (Savigny)
Allolobophora chloritica (Savigny)
Eisenia rosea (Savigny)
Octolasium lacteum Orley
Eiseniella tetraedra (Savigny)
Bimastos tenuis (Eisen)
Haplotaxis gordioides Hoffmeister (an aquatic form)

Distribution

Earthworms, like other invertebrates, are not distributed at random. Based upon observations made during the course of this study, the following 2 factors were found to be of great importance: first, the amount and diversity of humus materials present; and second, the amount of moisture present in the soil.

Both the total number of earthworms and the number of different species represented increase with the amount and diversity of humus and raw litter present. Diversity seems to be the more important of these factors, since in pure conifer plantations there was a heavy carpet of raw litter and humus from needles and branches, yet the number of earthworms was very low. This may indicate that decomposing needles are not satisfactory food for earthworms. The distribution of earthworms in such a stand roughly correlates with the amount and diversity of herbaceous ground cover.

In Table I the check marks indicate the presence of earthworms of the species indicated. The question marks show that one of the 3 species of the genus *Lumbricus* was present. Since all were immature, only the generic level could be determined with certainty. *Allolobophora chloritica* was found less than 50 feet from the edge of the old field type and this collection is therefore marginal. The numbers in the last column and on the lowest line indicate the numbers of species or habitats in which they were found.

This distribution agrees closely with that found by Murchie (1956) and correlates with the known relative tolerances of the species. Table I therefore reflects the ability of the various species to adapt to different environments.

Numbers and Importance of Earthworms

The number of species of earthworms tends to correlate with the diversity and amount of ground cover in the habitats: the greater the amount and diversity of plant life present, the greater the number of species of earthworms present. These factors seem to outweigh the kind of soil present although soil conditions have

DISTRIBUTION OF EARTHWORM SPECIES

	Al. calignosa	Ei. rosea	Oct. lacteum	L. terrestris	L. rubellus	E. tetraedra	Bi. tenuis	Al. chloritica	L. castaneus	H. gordioides	No. of Species
Old Field	✓	✓	✓	✓	✓		✓		✓		7
Stream Bank	✓	✓	✓	✓	✓	✓				✓	7
No. Hardwood	✓	✓	✓	✓			✓				5
White Pine	✓	✓	✓	?	?				?		4
Red Pine	✓	✓	✓			✓					4
Shores of Ponds	✓	✓	✓								3
White Cedar	✓			?	?				?		2
Norway Spruce											
No. of Habitats	7	6	6	4	2	2	2		1	1	

TABLE I. Distribution of Earthworm Species.

much to do with the amount and variety of plants living there.

The number of earthworms found in any cover decreased rapidly after the moisture content dropped below 20-25%. The lowest limit of moisture recorded in which an earthworm was found during this study was 7%. In this case the worm was in a state of aestivation, tightly coiled within a small walled cell. The water content typically was lower in the pure conifer stands than in adjacent mixed cover. Earthworms disappeared from these conifer stands, even in open herb-covered areas, before they did from areas covered with a mixed growth.

The largest number of earthworms was found in the surface layers in the spring when the water table was near the surface. Evidently they were compelled to move upward by the water.

During the summer as the surface soil became dry, the greatest numbers of worms were from 3 to 6 inches beneath the surface. At depths greater than 6 inches the number rapidly decreased and only the larger species were found. The following figures give the number per acre which is the unit used by many other writers dealing with earthworm population studies.

The number of earthworms per acre found in the top 6 inches of soil and their variation between types is very interesting.

Habitat	*Maximum*	*Average*
Old field	348,480	151,371
Northern hardwood	196,020	136,125
Red pine	381,150	119,790
Scotch pine	370,260	89,298
White pine	239,580	81,675
Norway spruce	0	0

The Scotch pine plantation was a young plantation in which the trees were under 3 feet in height and the ground cover still consisted principally of grasses and herbs. A Scotch pine plantation in which the crown had closed would present a much different situation.

The variation in number per species per acre is equally interesting, as shown in the following data.

Species	*Maximum*	*Average*
Allolobophora calignosa	653,400	90,387
Lumbricus terrestris	196,020	57,172
Octolasium lacteum	185,130	51,183
Eisenia rosea	119,790	46,827
Lumbricus rubellus	217,800	——
Bimastos tenuis	87,120	——
Eiseniella tetraedra	54,450	——

Table II gives 2 sets of figures needed to determine the relative abundance of each species based upon the numbers and distribution. The figures above the diagonal lines are the average numbers of specimens of the species that were found in those samples in which that species occurred. Those below are the frequency indices expressed in percentages.

RELATIVE IMPORTANCE OF EARTHWORM SPECIES

	Al. calignosa	Ei. rosea	Oct. lacteum	L. terrestris	L. rubellus	E. tetraedra	Bi. tenuis	Al. chloritica	L. castaneus	H. gordioides
Old Field	7 / 38	8 / 25	6 / 13	4 / 15	5 / 10		3 / 5	2 / 3	2 / 3	
Stream Bank	5 / 77	6 / 66	4 / 66	2 / 22	3 / 66	1 / 10				
No. Hardwood	4 / 33	2 / 19	2 / 23	1 / 36	1 / 36		5 / 4		1 / 36	
White Pine	4 / 21	3 / 21	2 / 14	1 / 14	1 / 14				1 / 14	
Red Pine	5 / 47	6 / 7	4 / 20	2 / 20	2 / 20				2 / 20	
Shores of Ponds	3 /	4 /	2 /	2 /						
White Cedar	2 / 33			1 / 33	1 / 33				1 / 33	
Norway Spruce										

TABLE II. Relative Abundance and Frequency of Occurrence of Earthworm Species in the Tully Forest.

The relative biological importance will actually differ from these figures for the following reasons:

1. The species differ greatly in size.
2. Their influence upon the environment may be different for different species.
3. Their food, host and parasitic relations may vary greatly between species.

Such a refined evaluation is beyond the scope of this paper.

The actual number of earthworms present in an area in the top 6 inches of soil was closely correlated with the amount of moisture present. When the soil moisture dropped the number of worms decreased. The present belief is that as soil loses its moisture earthworms burrow to deeper levels. Collections made during this study found a shift from the top inch or two to a depth of 5 or 6 inches but not to deeper levels. The larger, stronger species are believed to go to depths of 6 feet or over (Stephenson 1930). Certain species did wall themselves up at depths to one foot and aestivated or entered a state of torpor until more favorable conditions returned. The digging carried out during this study revealed so few animals at greater depths than one foot that it raises a question about the adequacy of this explanation. A limited amount of migration to more favorable sites was indicated. Moisture content was not determined for all samples and the lowest limit is not definitely known, although it seems to approach 7%.

This study was carried out from June through September, which includes the dry season of the year, when earthworms become scarce or absent in many areas. A similar investigation should be conducted from September to June to complete the picture. I believe the counts would be higher from September to June although the number of species should remain the same.

Discussion

The information collected during this study makes possible a more intelligent evaluation of earthworms as an important group of soil animals on the Tully Forest. We know what species we can expect to find, where, and in what numbers. We now need to know more about their relations to the plants and other animals in the area. To give but a few of these relationships: Earthworms ingest nematodes, fungi, bacteria and protozoa with their food and with the soil they pass through their digestive tracts. Several species in each of these groups are known to be pathogenic to plants or animals. Do the earthworms kill these organisms or simply transport them from the point of ingestion to the point where the castings are released? This may be a considerable distance. If the adults are killed, are any of the nematode eggs, fungal spores, and encysted forms still viable or are they also destroyed? If earthworms are vectors for any of these organisms, how rapidly could they spread the forms concerned by their travels from place to place? How far and how rapidly do earthworms move? Are they important control agents that destroy desirable or undesirable organisms?

One known example may suffice. Bunyea (1931) tells us that earthworms may play an important part in the spread of the roundworm causing gapes in poultry. The infective eggs or the young gapeworms which have hatched in the soil from eggs in the fowls droppings may be eaten by earthworms; they burrow into the body muscles of the earthworm and may remain alive for considerable periods. The earthworm in these cases is not a necessary intermediate host of the parasite; it is merely a mechanical carrier or reservoir, protecting the young gapeworms. They may thus carry the young gapeworms over from one warm season to another. When the earthworm is eaten the gapeworms complete their life cycle in the fowl.

To illustrate another relationship, Barker (1958) considers earthworms biological concentrators of DDT, and, since they constitute an important part of the food of many species of birds and a few species of mammals, their consumption may be lethal to these species where sprays are used even though the dosage of DDT is too small to be effective directly. Earthworms are important food items for many other animals such as frogs, toads, salamanders, shrews and moles. Food chains are very important and need much further investigation.

The direct actions of earthworms not only increase porosity and friability of the soil by their tunnels and castings but they also carry on all metabolic activities. They use oxygen and give off carbon dioxide and other waste products. Some of these waste products are high in nitrogen content and in a form usable by other plants and animals. They reduce raw humus and other substances passed through their digestive systems, both chemically and physically, to smaller units and more simple compounds. The total effect of these processes may not be great for a single worm, but when multiplied by several hundred thousand individuals per acre the effect is considerable.

This general survey has set the stage by telling us what earthworm actors we have on the forest, where they are found and in what numbers. It furnishes information essential in interpreting the importance of earthworms when we know the role they play in relation to other soil flora and fauna.

Dr. James A. Larsen (1956, page 101) makes a statement I should like to quote in conclusion:

> "We are, thus, quite familiar with the multitude of species that make up the living world. But we have only begun to study the ways by which plants and animals live as individuals and as part of the world of life. . . . With greater understanding of what happens within the living organism, there will be greater opportunity to understand the relationships existing between the plants and animals—and human beings—that make up the living world."

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INTERPRETATION OF VARICES AND GROWTH RIDGES ON SHELLS OF *EUPLEURA CAUDATA*[1]

In some bivalve mollusks, growth ridges are formed annually and can be used to determine age. For example, the Pismo clam (Weymouth 1923), the Pacific razor clam (Weymouth, McMillin and Holmes 1925), and the Pacific cockle (Weymouth and Thompson 1931) can be aged accurately by counting shell ridges. To my knowledge, only Magalhaes (1948), who found that from none to 3 growth ridges a year are formed on shells of *Busycon canaliculatum* and *B. carica* with no apparent relationship to age, and Clarke (1956), who states without experimental evidence that ridges on shells of *Nassarius trivittatus* probably have no relationship to age, have treated this subject with regard to snails. Cole (1942) attempted to assign ages to smooth oyster drills, *Urosalpinx cinerea*, by counting ridges on the siphonal canal, but he did not determine beforehand whether they were correlated with age. Andrews (1956) questioned Cole's conclusions on this account.

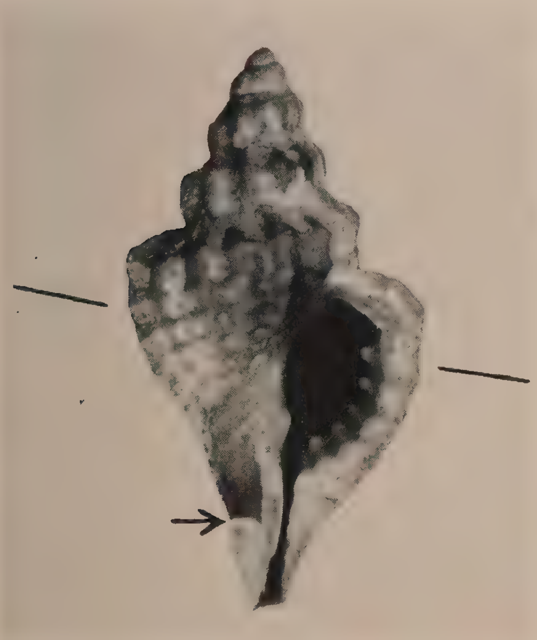

FIG. 1. Shell of *Eupleura caudata*. Arrow points to siphonal canal growth ridge. Lines at left and right show where shell was cut for Figure 2. Shell measures 22.0 mm in height.

It might be suspected that growth ridges on certain snails do not represent yearly markings because the distance between successive growth ridges is usually considerably smaller than yearly increments in growth. For example, recent observations at the Virginia Fisheries Laboratory of the rough oyster drill, *Eupleura caudata,* show that, whereas the distance from the siphonal growth ridge to the tip of a fully grown siphonal canal where the next growth ridge would appear may measure 2 to 6 mm, shell growth may exceed 10 mm a year (Figure 1).

Records of individual *E. caudata* actually showed that these snails do not deposit a consistent number of varices and siphonal canal ridges per growing season (Figures 1 and 2). Growth of this drill in Virginia waters extends from about the beginning of May to the end of October. In contrast to *U. cinera* which may have several or many small and usually poorly-defined growth ridges on its siphonal canal, *E. caudata* usually has one prominent ridge. When the first varix has been laid down, when the drill is 10 to 15 mm high, there is no ridge on the siphonal canal. After this, shell growth usually occurs as half-whorl increments. A thin layer of new shell material is deposited through an arc of 180° and then it flares out to form another varix. While this layer is being reinforced from the inside with successive layers of new shell, there is growth neither laterally at the varix margin nor longitudinally at the siphonal canal tip. It takes approximately 7 weeks to form and reinforce a half whorl. With its formation, a new growth ridge which consists of a line of demarcation between the tip of the old siphonal canal and the new shell appears on the new siphonal canal. Varices and growth ridges are formed with each successive half whorl of growth and old ridges are grown over.

In May 1956, 60 drills, having at least one varix and measuring in height from 12.8 to 26.2 mm, were caged and examined once a month until fall 1957, *i.e.* through 2 summers and a winter. The cages consisted of wooden frames with plastic screen sides and top (4 holes to a linear inch) and plastic screen bottoms (8 holes to a linear inch). The cages were 37 inches long, 16 inches wide and

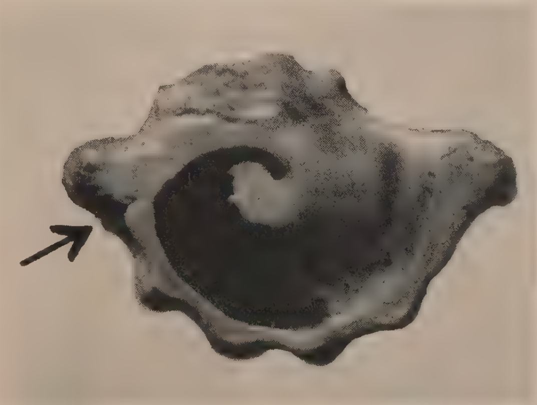

FIG. 2. Shell cut approximately perpendicular to longitudinal axis. Prominent ridges at left and right are varices. Four smaller ridges at bottom are axial ribs. Arrow points to place where growth of last half whorl of shell began. Shell grew in counterclockwise direction from here and stopped at varix on right.

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[1] Varices are prominent ridges parallel to the margin of the aperture on shells of certain snails. This research was conducted under a contract at the Virginia Fisheries Laboratory with the U. S. Fish and Wildlife Service, No. 14-19-008-2372, Study of Oyster Drills in Chesapeake Bay.

6 inches deep, and included 8 compartments 9 x 8 x 6 inches. For support and stability they were tied into seasoned, tarred sea-rac oyster trays (Hewatt and Andrews 1954) and suspended in the York River along the laboratory pier one foot from the bottom with from one to 3 feet of water covering them. A male and female drill were kept in each compartment with several one- and 2-year old oysters for food. Although ages of the drills were unknown, it is probable that both young and old drills were included in the experiment because their heights matched almost the full range of heights of hundreds of drills collected randomly from nature.

Most mature drills in cages did not grow either summer because growth of *E. caudata* usually ceases with the onset of sexual maturity (unpublished data). Mature females were considered as those which deposited embryo cases during the experiment. Immature females did not deposit cases. Mature males had a full-size penis. Growing drills did not form a consistent number of half whorls and coincident varices and siphonal growth ridges per growing season. Eight individuals each formed 2 in one summer, apparently a normal number because many wild drills collected in late summer near the cages also showed 2 half whorls which appeared to be newly formed. Seventeen caged drills deposited just one half whorl a summer, but only 2 of these grew during both summers. A single caged drill deposited 3 half whorls. Several drills died or were lost during the experimental period.

It is clear that varices and siphonal growth ridges on shells of *E. caudata* cannot be regarded as yearly formations and probably have little value in determining age of drills.

I wish to thank Dr. William J. Hargis, Jr. for guidance during this study, and Dr. J. D. Andrews for critically reading this paper.

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THE AVAILABILITY OF A MINIATURE BOMB CALORIMETER FOR ECOLOGY

A miniature bomb calorimeter, described by McEwan and Anderson (1955), is now being tested with reference to biological material at the University of Michigan. Individual samples of biological material as small as 6 mg can be burned and estimation of calories released on complete combustion can be provided with an error of the order of 5% (1% on larger samples).

Data of this type may be of value for two reasons:

1. Studies of population and community energetics rely heavily on caloric determinations (discussed in Slobodkin 1960).
2. There is intrinsic evolutionary interest in the distribution of calories per gram among animals.

It seems advisable to burn as wide a variety of microfauna samples as possible, while the bomb is available. We will, therefore, attempt to provide caloric analyses in exchange for appropriately prepared and labeled samples of microfauna (*i.e.* animals of less than 50 mg dry weight). No more than 3 or 4 analyses can be made in a working day, so that we can not guarantee rapid results, but we will try to keep up with the demand.

Samples should be accompanied by complete taxonomic and collecting data.

Frozen dried material is best. Alternatively, samples may be dried for 24 hours at 60° C in a vacuum oven and mailed in screw topped vials or weighing bottles. Low drying temperatures are advisable to prevent loss of volatile, energy rich, compounds. A period of starvation prior to drying will help avoid contamination with gut contents.

Any chemical analyses of duplicate samples to those burned in the bomb would be of great value. Combustion train analysis for C, H and N would permit approximate weighting for the protein, carbohydrate, fat ratio (Spoehr and Milner 1949).

Our results will be expressed as cal/gm.

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A CRITIQUE OF THE HEAT UNIT APPROACH TO PLANT RESPONSE STUDIES[1]

Introduction

The "heat unit approach," in use for over two centuries, is a scheme for studying plant-temperature relationships by the accumulation of daily mean temperatures above a certain threshold temperature during the growing season. If a plant has a base temperature of 40°F and the mean temperature on a given day is 55°F, the difference in degrees for that day is termed "degree-days" or "heat units."[2] In this example, we would have 15 degree-days. If 1200 degree-days are required for maturity, the plant should reach maturity by the time 1200 degree-days have been accumulated. This sum required for a particular crop variety has been assumed by heat unit workers to be a constant value and is termed the varietal constant. By knowing the varietal constant, users predict the date on which their crops should be harvested. This linear relationship, known as the "remainder index method," gave rise to a number of expressions, such as "degree-days," "heat units," "growing degree-days," "growth units," and others relating plant responses to season thermal levels.

Review of Literature

Since much of the valuable work done in the past 230 years has been neglected by many modern users, a world-wide survey of major contributions to the heat unit approach is in order.

Around 1730, René A. F. de Réaumur invented a temperature scale in which 0° marks the freezing point and 80° the boiling point of water. Although his temperature scale, known as the Réaumur scale, is now almost obsolete, except among some cheese-makers, his ideas on the quantitative study of plant-temperature relationships are worthy of mention. He summed up the mean daily air temperatures for 91 days during the months of April, May and June in his locality and found the sum to be a nearly constant value for the development of any plant from year to year. This summation of temperatures, published in 1735, was later known as Réaumur's thermal constant of phenology. He assumed that his thermometric constant expressed the amount of heat required for a plant to reach a given stage of maturity. This idea gave rise to the heat unit system of today.

Others have adopted Réaumur's idea as a basis for their own indices. Adanson (1750) borrowed it but disregarded all temperatures below 0°C and took only the sums of positive temperatures on the Centigrade scale. This resulted in the establishment of a "remainder index method." In considering sunlight as an important physiological factor, Humboldt (1794-1845) initiated the idea of the actinometric constant. Boussingault (1834) found that the length of the period from germination to any given stage is inversely proportional to the sum of the daily temperatures above 0°C during that period. Edwards and Colin (1834), studying germination, called attention to the upper limit of plant growth in calculating the thermal sum. Gasparin (1844) considered the influence of sunlight and conducted studies on the thermal constant above 5°C occurring from planting to harvest of cereals. Fritsch (1852-1871) adopted Kabsch's (1863) reasoning on plant growth and formulated the following thermal constant:

$$x = t \pm (ht/12)\, c - C$$

All the above symbols, except C, indicate a summation of one phase to the next, such as germination to flowering, of which x is the thermal constant; t is the total number of days; c is the total sum of mean daily temperatures; and h is the average number of hours from sunrise to sunset for the period concerned. C is the total heat sum between planting and germination. In 1861, Fritsch determined thermal constants for the blossoming and ripening of 889 different plant species. This was done by totaling the mean daily temperatures above 0° Réaumur from January 1 onward. Sachs (1862) confirmed the importance of both the upper and the lower limit of plant growth by experimentation. Linsser (1867, 1869) published results of a larger and somewhat more mathematical study using Bessel functions. He concluded that a given plant species reaches the same stage of vegetative development from year to year by the time the same mean daily temperature is reached. Similar relationships were found to hold when the same sum of the mean daily temperatures above freezing was reached and also when the sum of the squares of these positive temperatures reached a certain constant value. Marié-Davy finally established the idea of the actionometric constant in 1873. Coutagne (1882) believed that the plant growth rate (v) depends upon a certain maximum temperature, which is assumed to be determined by sunlight, wind and moisture. It diminishes as that temperature approaches the freezing point of water. Thus,

$$v = ae^{-[(x-c)/n]^2}$$

where a is the coefficient of the rate of development, e is the base of natural logarithms, x is the plant temperature, c is the optimal temperature and n is the coefficient of the sensitivity of plant response. Hence, the total growth, L, is expressed as

$$L = \int_{x_1}^{x_2} ae^{-[(x-c)/n]^2}\, dx$$

The reciprocal of a defines the longevity of a plant, while c and n determine the temperature range of plant acclimatization and x_1 to x_2 represent the temperature range under consideration. Angot (1882-1890) studied a group of plants, using a more elaborate thermal sum approach than that used earlier. Price (1909) emphasized the application of the van't Hoff—Arrhenius principle in the study of physiological constants and established an exponential index. Livingston (1913) worked out a scale of weighted temperature values between 40° and 90°F. Later, he made use of Lehenhauser's (1914) observations on the rate of elongation of maize seedlings at different temperature levels, and in 1916 devised a new index called a "physiological summation index." His index u is represented as

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[1] This study is jointly supported by the Continental Can Company, The American Can Company and the U. S. Weather Bureau. Gratitude is expressed to Professors V. E. Suomi, Department of Meteorology, University of Wisconsin; and to J. E. Newman, Department of Agronomy, Purdue University.

[2] It is necessary to distinguish the terms "degree-days" or "heat units" and "heating degree days." The former is the summation of temperatures above a certain threshold value and is used in studies of plant-temperature relationships; the latter is the summation of temperatures below a certain limit value and is used in studies on heating design and engineering. Climatological data of the U. S. Weather Bureau designated as "degree-days" refer to the latter.

$$\log_2 u = \frac{(T\text{-}40)}{18}$$

where T is the temperature in degrees Fahrenheit, 40 is the threshold temperature and 18 is a constant based on the van't Hoff—Arrhenius principle.

Many workers have applied the "remainder index method" to numerous native and cultivated plants over the past four decades. A cross-section of these researchers since 1919 is listed in Table I.

Table I. A Cross Section of Remainder-Index Method Researchers, 1919-1952

Year	Researcher	Plant	Contribution
1919......	Kincer	Wheat	Regional studies in USA; base temperature 43°F
1921......	Appleman and Eaton	Sweet corn	Summing daily mean temperatures to ripening
1924-34...	Boswell	Peas Spinach	Base temperature 36°F for peas and 42°F for spinach
1931......	Winkler and Williams	Grape	Maturity test
1944......	Baker and Brooks	Apricots, plums	Number of days required from flowering to harvesting
1946......	Scott	Peas, corn	Quality control
1948.....	Seaton	Peas	Scheduling of planting
1948......	Barnard	Tomatoes	Base temperature 50°F
1948......	Bomalaski	Peas	Growing degree day
1950......	Gould	Snap beans	Base temperature 50°F
1951-52...	Lana and Haber	Sweet corn	Degree-hour summation

In 1948 Nuttonson attempted to improve the remainder index approach by applying the concept of the "photothermal unit" or P.T.U. in climatic analogue studies. This has been expressed by Wang (1958 as

$$PTU = \sum_{i=D_p}^{D_m} (\bar{T} - T_c)t_s$$

where D_p is the date of planting, D_m the date of maturity, $\bar{T}$ the daily mean temperature, T_c the critical temperature and t_s the day length in hours.

Lindsey and Newman (1956), in a study of the flowering dates of native plants, attempted to improve the simple daily mean method of accumulating heat units. Their method of temperature summation is based on the diurnal spread and was designed to reflect the approximate durations of different temperature levels during the statistical day. The effective diurnal spread is converted into degree-hours (DH) and can be expressed as

$$DH = \frac{12(h\text{-}t)^2}{h\text{-}w}$$

where h is the daily maximum temperature, w is the daily minimum temperature and t is the base temperature.

Padol'skiĭ (1958), studying the phenology of cotton in the USSR, found that neither the heat sum nor the threshold temperature is a constant value. By constructing a pheno-temperature nomogram to eliminate this nonlinearity, he achieved a greater accuracy in phenological prognosis.

Holmes and Robertson (1959) introduced a generalized formula for the computation of weekly degree-days above 42°F for nine stations in Canada. Their formula is

$$\bar{D} = N\,[(t\text{-}b) + L\sigma/\overline{N}]$$

where $\bar{D}$ is normal degree-days accumulated for the months concerned, N is number of days in a month, t is monthly mean temperature, b is base temperature, 42°F, L is a proportionality coefficient and σ is standard deviation of monthly mean temperature. The coefficient L can be obtained from a table prepared by Holmes and Robertson in 1959.

Arnold (1959), in his determination of significance of the base temperature in a linear heat unit system, found that the base temperature commonly used was too high. He made a regression equation from temperature and the rate of development. The equation is solved for the temperature when the rate of development is zero. The temperature obtained is defined as the base temperature.

Although enormous work has been done in heat unit studies, there has been little integration of such work. Consequently, further investigation and understanding of the results of past research are necessary.

Application

In the past three decades, the heat unit system has been adopted by many in the canning industry, especially as a means of scheduling planting dates to insure an orderly flow of raw materials of optimal maturity to the cannery. Further applications have been scheduling spraying programs for insects, disease and weed control. The system is also of use in the selection of suitable farming areas and of appropriate crop varieties for these areas.

Researchers have applied this system to a wide variety of plants, both native and cultivated, and have made many refinements in the methodology. The results have been correlated with various phenological events of the plants studied. Also, entomologists, plant pathologists, ornithologists, zoologists, and others have used the system in their fields of investigation.

The heat unit system has been widely adopted because of its value in satisfying practical needs, rather than for its accuracy or its theoretical soundness. Because no other system has been found which can adequately replace it, it continues to enjoy widespread popularity.

Criticism

In spite of the many applications and intensive investigations conducted over two centuries, the heat unit system has been subjected to serious criticisms, particularly in recent years. Even its faithful users in the canning industry have found flaws in the system and are seeking means of improvement. Its disadvantages may be summarized as follows:

(1) Plants respond differently to the same environmental factor during various stages of their life cycle. Varietal constants obtained from heat unit computations fail to take into account these time sequences. For example, Alaska-type peas yield well in Wisconsin if grown under warm spring conditions during seedling stage and cool summer at their reproductive stage. Under the opposite environmental conditions (i.e., in cold springs and hot summers), a poor yield results. This is illustrated schematically in Fig. 1. Here, area ABC represents the summation of the daily temperatures above 40°F in the

case of a cold spring followed by a hot summer, while the area DEFC represents that of a warm spring and cool summer. Since areas DEOA and OBF are equal, the heat sums for both cases are identical and neither can be used to differentiate the time sequences of plant responses to temperature. In those years in which this situation occurs, the heat unit system would not work. For example, a study of the monthly temperatures of Ethiopia, known as the pea-producing center of the ancient world, shows that only very small temperature changes occur from month to month (Wang and Bryson 1956). From January to April, the temperature line for Ethiopia is flatter than line EOF in Figure 1. Thus the orientation of line EOF further toward the horizontal might indicate a better pea-producing season.

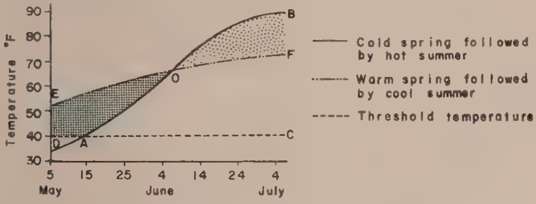

FIG. 1. Schematic Diagram of Heat Summation.

(2) The threshold temperature as it was employed in heat unit computations is considered a constant, applied to the entire life cycle of a plant. The generally accepted value for the threshold temperature of peas is 40° F and that for corn is 50° F. This is unsound, since the threshold values change with the advancing age of the plant, as shown in Figure 2, Wang and Bryson (1956). Moreover, the upper threshold is not taken into account. Sacks, as early as 1862, confirmed the importance of both the upper and lower threshold temperature through experimental results.

(3) Thornthwaite (1952) pointed out that when all possible threshold values from 32° to 50° F were tested systematically, none was found which would give any improvement in the heat unit system. Various upper temperature limits were also tested in the same way and no better findings resulted. Neither was Wang (1957) able to achieve any improvement in the system by making heat unit summations over growing periods of various lengths. Padol'skiĭ (1958) too reached the same conclusion in his study of cotton plants.

(4) Daubenmire (1947) pointed out that the heat unit requirement of a given process is constant only for that range within which a direct proportionality exists between growth rate and temperature. A lack of such proportionality is usually found near the upper and lower threshold temperatures. Moreover, over the growing season the growth of a plant is a continuous function; thus, the growth versus time is sometimes a near-linear function. This function is similar to the summation of heat units versus time. Because of their linearity these two physiologically unrelated factors[3] sometimes happen to coincide.

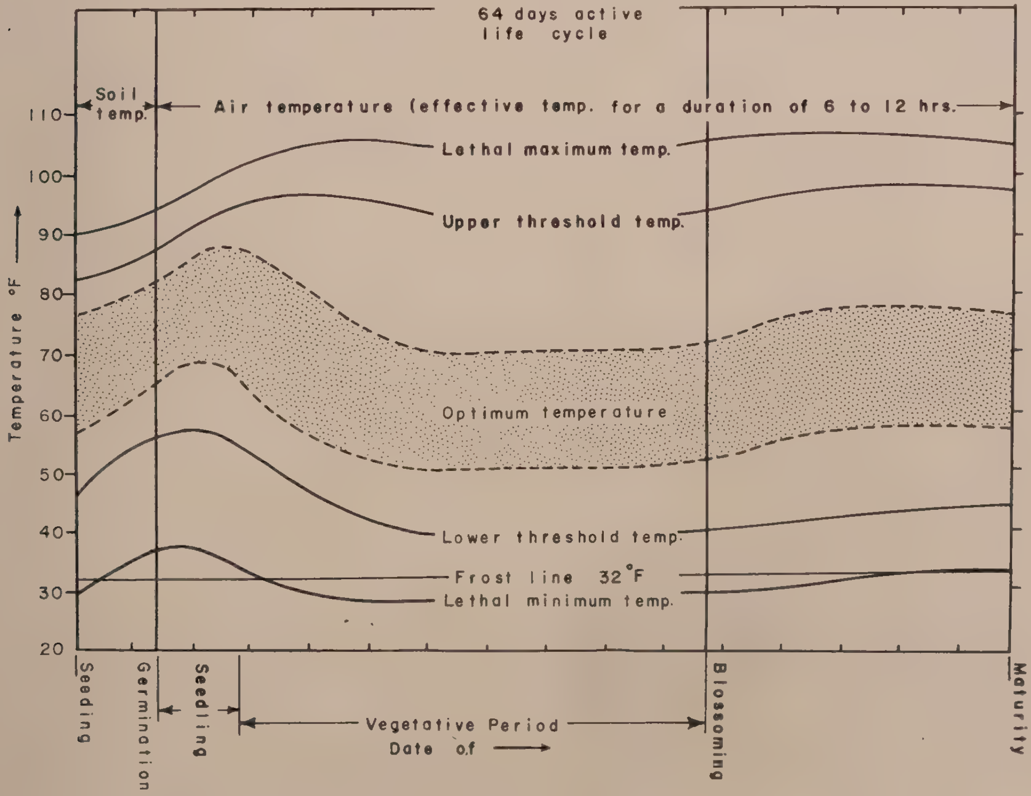

FIG. 2. Thermal responses of canning peas.

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[3] We refer here to the heat sum and not the temperature itself. Heat sums average out and thereby disguise the singularity of temperature changes.

Usually, however, the temperature responses in terms of the growth curve are sigmoid and not linear; in fact, the extreme high temperatures to which plants are sometimes subjected have negative effects on their rate of development. Padol'skiĭ found that when the optimal temperature for growth is reached, the heat sum is no longer linear.

(5) The heat unit system does not take into account many factors which influence plant growth and development, such as soil moisture, vapor pressure deficit, etc. Some workers have pointed out the importance of environmental factors other than temperature: for example, sunlight by Gaspirin (1844); solar radiation, wind and moisture by Coutagne (1822); and duration of light by Nuttonson (1948). Even the exponential heat sums of Livingston (1916) and Katz (1952) are valid only between the upper and the lower threshold temperatures for a given crop variety, since above or below these thresholds the van't Hoff—Arrhenius' constant no longer applies. The heat unit system is usually computed on the basis of the mean daily temperature and does not take into account the effects of the extreme day or night temperatures, the interdiurnal temperature changes[4] and the difference between day and night temperatures.

(6) Finally, the microclimatic problems regarding the representative quality of the temperature records used for heat unit evaluations are among the most complicated problems yet to be solved.

CONCLUSION

To improve the heat unit system:

(1) Representative temperatures should be taken. The height of observations should vary from time to time according to the height of the plants. Observations should be made at random in various locations throughout the field. The number of locations to be sampled would depend upon the size and topography of the field as well as the variation in its microenvironment.

(2) The threshold temperature used should be changed according to the age of the plants, as indicated in Figure 2. The upper threshold limits also need to be considered. A quantitative evaluation should be made of the negative effects of temperatures beyond the threshold values for both upper and lower extremes. The length of period for the accumulation of temperatures using any one threshold value should not be more than a week. More phenological events should be recorded in order to accommodate the short period of temperature accumulation.

(3) Growth and development[5] should be differentiated. For example, flowering is a developmental event, while the height of a plant is a result of growth processes. For example, determining the maturity date of sweet corn involves a problem of morphological development. By observing various growth stages, researchers found that subterranean ears initiated on underground portions of the stem will later become functional ears if soil temperatures soon after planting are favorable. Figure 3 shows how soil temperatures during the first two weeks after planting "predetermine" the later development of the ears (Wang 1958b). The curve shown, which is based on 13 years' study, can be used as a basis of predicting maturity dates. This is possible because only developmental processes are involved; had growth processes been a factor, such a method would not be applicable.

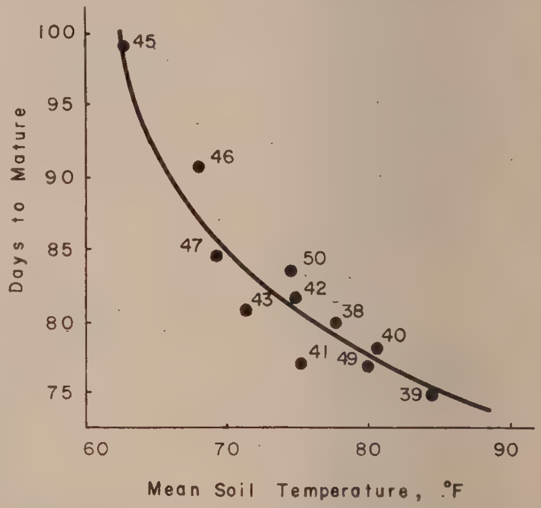

FIG. 3. Duration of the Growing Season for Sweet Corn (Ioana Variety) at Ames, Iowa. (mean soil temperature at one inch depth, 1938-1950). Numbers accompanying the dots represent years during 1939-1950.

(4) The environmental parameter should be adjusted. For example, Wang (1958a) studied the effect of a combination of warm day and warm night during the significant period of 31 days prior to maturity on the yield of sweet corn. The effective air temperature (E) in degrees Fahrenheit, thus defined, can be formulated as

$$T_E = \sum_{i=d} (T_D - 70) T_{M > 70} + \sum_{i=d} (T_N - 50) T_{M > 50}$$

where T_D is the is the average day temperature between sunrise and sunset when T_M is greater than 70° F; T_N is the average night temperature between sunset and sunrise when T_m is greater than 50° F; T_M is the hourly maximum temperature of the day; T_m is the hourly minimum temperature of the night; d is the number of days. In computing the average day or night temperature, one considers only the times when the maximum hourly temperature of the day (T_M) or the night (T_m) is above 70° F or above 50° F, respectively. This type of formulation is valuable because it describes certain characteristics of environment which are of biological significance, and indicates environmental data should be adjusted.

Other formulations for the computation of heat units other than the remainder method are useful but have not been widely adopted. Examples are: Fritsch (1861), Linsser (1867), Coutagne (1882), Livingston (1913), Nuttonson (1948), and Lindsey and Newman (1956).

The non-linearity of plant-environmental relationships should be corrected. Wang (1958a) has established a "sorter" as the first approximation which has the adjusted environmental parameter as the ordinate and the plantings as the abscissa, as in a rectangular coordinate system. Crop events, such as yield data, are classified as those of "much above normal yield" as well as "much

[4] The interdiurnal temperature change is defined as the difference between the maximum temperature of one day and the minimum temperature of the following day.

[5] Growth refers to the increase in weight or volume of a certain organ of a plant as a whole, occurring within the time interval of a phase. Development is the appearance of a series of phases of a plant during its life cycle.

below normal yield" while disregarding all normal yield data. If sorting were done for one parameter at a time, one could eventually determine: (1) which parameter is more important, (2) how crop yield is related to changes in temperature, (3) how the temperature-yield relationship is affected by the existence of the other environmental factors, and (4) how much non-linearity exists. Of course, there are several methods which could be employed for solving the problem of non-linearity (Katz, 1952; Podol'skiĭ, 1958).

(6) The environmental parameters, such as rainfall and temperature, should be combined. Before this can be done, rainfall and temperature must be reduced to a common unit and each weighted as to crop response. Wang and Bryson (1956) drew "same rainfall lines" (isohyetals) in a single chart with rainfall as ordinate and year as abscissa. They set a base line on the opposite end of the ordinate, parallel to the abscissa, and measured the distance between the base line and one of the isohyetals for each year, expressing the measurement in inches. By repeating this process with temperature data, the "same temperature lines" (isothermals) were drawn. Again, the distances were measured and expressed in inches. By doing this, they combined two unrelated units. By determining the statistical significance of the plant responses to one factor versus the other factor, a weighted value can be obtained. Also, the sorting device, as has been mentioned above, will serve the purpose.

Greater familiarity with available literature dating back to 1735 and wider adoption of these improvements should advance further the study of plant-temperature relationships.

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GENETIC VARIATION IN THE WINTER CHILLING REQUIREMENT FOR DATE OF DORMANCY BREAK FOR *ACER RUBRUM*

INTRODUCTION

Most tree species from the temperate climate must be exposed for a minimum number of hours to low temperatures (for chilling treatment) before they can break their winter dormancy in a normal fashion. Unless peaches, apples, blueberries, and similar crops are exposed for a minimum number of days to temperatures below a maximum of 30-40°F the plants will not break dormancy or fruit properly. This chilling requirement is a factor that prevents successful cultivation of many deciduous species and varieties in the warm climate of the southern U. S. Plant breeders have striven to modify the winter chilling requirements of favorite peach varieties by introducing genes of low chilling requirement from tropical and subtropical varieties. These attempts are meeting with some success (Weinberger 1950, Lesley 1944). With the expansion of tree planting programs the possibility of genetic variation in winter chilling requirements is of economic importance and theoretical significance. This paper describes an investigation of the pattern of genetic variation in the chilling requirement of red maple, *Acer rubrum* L.

Winter chilling requirements are recognized for forest trees as well as for horticultural species. Olmsted (1951) investigated the photoperiod and chilling requirements of progenies of sugar maple trees and found some variation in the chilling requirement of *Quercus macrocarpa* Michx. Olson et al. (1959) conducted similar investigations on the chilling requirements of eastern hemlock, *Tsuga canadensis* (L.) Carr.

The literature reviews by Doorenbos (1953), Samish (1954), Vegis (1955), Wareing (1956), Weinberger (1950) and the works of Howard (1910, 1915a, 1915b) give a good coverage of the genetics, the physiology and the variety of species that possess chilling requirements.

The authors wish to thank those who made seed collections for this study: A. J. Carmichel and M. Holst—Ontario Dept. of Lands and Forests; D. B. Cook—New York Conservation Department; W. Gabriel and B. Zak—U. S. Forest Service; A. Johnson—University of Minnesota; P. J. Kramer—Duke University; H. B. Kriebel—Ohio Agri. Exp. Sta.; T. R. Phillips—New York State Ranger School; R. G. Ray—Canada Dept. of Northern Affairs and Natural Resources; M. Stoddard—Virginia Forest Service.

MATERIALS AND METHODS

Red maple is an ideal tree for investigation of the pattern of genetic variation in winter chilling requirement. It ranges from Canada to the Everglades of Florida, and throughout the eastern U. S. Within this range the frost-free season varies from less than 100 days in northern Maine and Canada to 365 days in southern Florida. A collection of red maple seed was made from individual mother trees from different points within this region. Whenever possible, from 2-4 mother trees were used to represent a given geographic locality. The collection points are indicated on the map (Fig. 1).

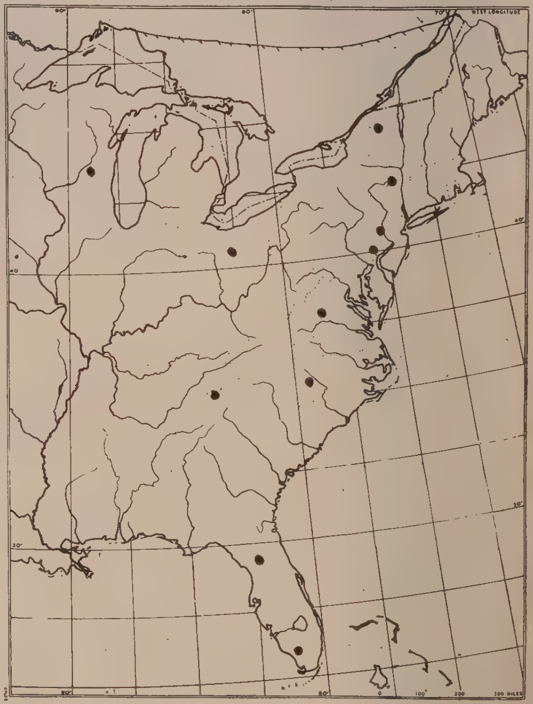

FIG. 1. Map showing where red maple seed collections were made.

Seedlings from these collections were raised in pots at Gainesville, Florida. On Jan. 3, 1957, after a year of growth, the progeny from each mother tree was divided into 4 equal lots. One lot was kept outdoors in the normal, mild winter climate of Gainesville. A second was put in an unheated greenhouse for the winter. The third was placed in a 34°F cold room for one month, and the remaining lot was placed in the same cold room for 2½ months. After the treatments the 4 lots were observed in the experimental forest genetics nursery of the University of Florida. The seedlings that had received one month of cold treatment were moved to the nursery on February 4. Seedlings from the greenhouse and from the 2½ month cold treatment group were moved to the nursery on March 21. Weekly observations were made to determine when 80% of the plants of each parentage and treatment had opened their buds and unfolded their first leaves, at which time the entire lot was arbitrarily recorded as being in active growth, i.e. it had broken dormancy.

EXPERIMENTAL RESULTS

There was no difference in the date of break of dormancy for the plants grown in the greenhouse for one month and the plants grown outside in the nursery. Therefore, only the dates of the break of dormancy for the plants kept in the nursery are recorded in Table I. The winter of 1956-57 was mild in Gainesville, and except for one or two cold nights when the temperature dropped below freezing there was no heat in the greenhouse during the experimental period. Hence there was little difference between the greenhouse temperatures and the temperatures in the nursery. This may account for the uniform behavior of the two groups of plants.

TABLE. I. Summary of dates of the start of active growth by the red maple progenies used. The frost-free seasons are the averages for the weather stations nearest the place of seed collections

Accession Number	Approximate Geographic Origin	Frost Free Season	Date of Start of Active Growth		
			No Chilling	1 Month Chilling	2½ Month Chilling
33-55	Gainesville, Florida	285	Feb. 20	Feb. 20	April 15
34-55	Gainesville, Florida	285	Feb. 20	Feb. 20	April 15
35-55	Gainesville, Florida	285	Feb. 20	Feb. 20	April 15
64-55	Durham, North Carolina	201	Apr. 22	Apr. 7	April 15
65-55	Durham, North Carolina	201	Apr. 7	Apr. 7	April 15
69-55	Gainesville, Florida	285	Feb. 20	Feb. 20	April 15
70-55	Gainesville, Florida	285	Feb. 20	Feb. 20	April 15
71-54	Norristown, Pennsylvania	189	May 15	Apr. 15	April 15
72-54	Norristown, Pennsylvania	189	May 15	Apr. 15	April 15
73-54	Norristown, Pennsylvania	189	May 19	Apr. 22	April 7
74-55	Wooster, Ohio	152	May 29	Apr. 22	April 22
75-55	Wooster, Ohio	152	May 29	Apr. 22	April 22
76-55	Wooster, Ohio	152	May 19	Apr. 7	April 22
81-55	Wind Gap, Pennsylvania	144	May 22	Apr. 15	April 22
92-55	Charlotsville, Pa.	213	May 6	Apr. 15	April 22
93-55	Stephentown Center, N.Y.	174	May 6	Apr. 7	April 15
102-55	Bryson City, N.C.	171	May 29	Apr. 15	April 22
151-55	Wanakena, New York	111	May 29	Apr. 22	April 22
152-55	Wanakena, New York	111	May 29	Apr. 22	April 22
153-55	Wanakena, New York	111	May 29	Apr. 22	April 22
154-55	Wanakena, New York	111	May 29	Apr. 22	April 22
308-55	Ochopee, Florida	365	Jan. 15	Feb. 8	April 7
309-55	Ochopee, Florida	365	Jan. 15	Feb. 8	April 7
310-55	Ochopee, Florida	365	Jan. 15	Feb. 8	April 7
311-55	Ochopee, Florida	365	Jan. 15	Feb. 8	April 7
312-55	Waukeshaw, Wisconsin	169	May 29	Apr. 22	—

The plants receiving cold treatment behaved quite differently from the greenhouse and open-grown plants (Table I). Plants from the Everglades of Florida broke dormancy without any chilling on January 15, while the dormancy until February 8. Chilling treatment hastened the break of dormancy for plants from more northern latitudes. Thus, plants from Wanakena, New York, broke dormancy one-month chilling treatment delayed the break of dor- on April 22, and grew normally when they received chilling treatment. Without chilling treatment less than 25% of the plants had broken dormancy by May 29 after the onset of the hot weather of 85-95°F. The growth of the unchilled plants was highly abnormal. No terminal buds developed, and basal and lateral buds sprouted to give rise to a sucker type of growth.

The experimental plants were photographed during the latter part of May, 1957. Figure 2 shows chilled and unchilled plants from parent 152-55, which is at Wanakena, N. Y. The chilled plants broke dormancy and grew normally. All the unchilled plants were dormant at the time the photograph was taken. Figure 3 shows the plants of parentage 72-54 from Norristown, Pa. The chilled plants broke dormancy on April 15, and grew normally, while the unchilled plants of the same parentage developed only sucker shoots. This sucker type of growth appears to be characteristic of plants that have not received adequate chilling treatment. Figure 4 shows plants of parentage 308-55 from the Everglades swamp in southern Florida. These plants had no chilling; they broke dormancy on January 15 and grew normally. The chilling treatments delayed the break of dormancy for the Florida plants. The chilled and unchilled red maple plants from the vicinity of Durham, N. C. (parentages 64-55 and 65-55) broke dormancy at approximately the same time, but the unchilled plants tended to form suckers similar to those of the unchilled plants shown in Figure 3.

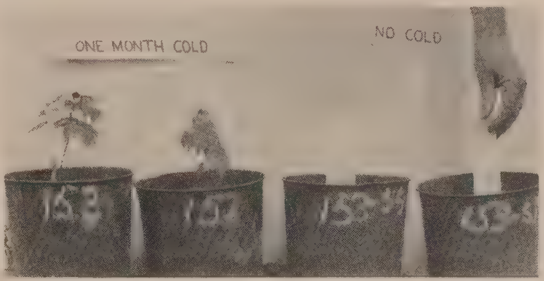

FIG. 2. Chilled and unchilled red maple plants from Wanakena, N. Y. All plants are from the same mother tree.

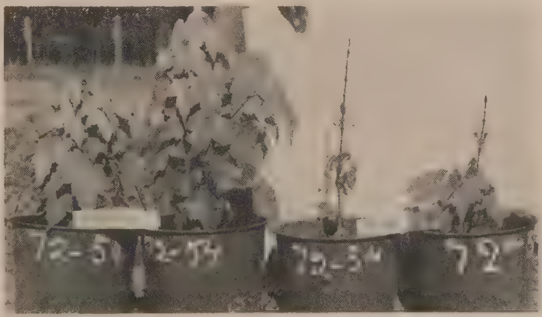

FIG. 3. Chilled and unchilled plants from mother tree 72-54 (Norristown, Pa.). The unchilled plants on the right did not break dormancy properly. Basal and lateral buds developed first to produce a sucker type of growth habit.

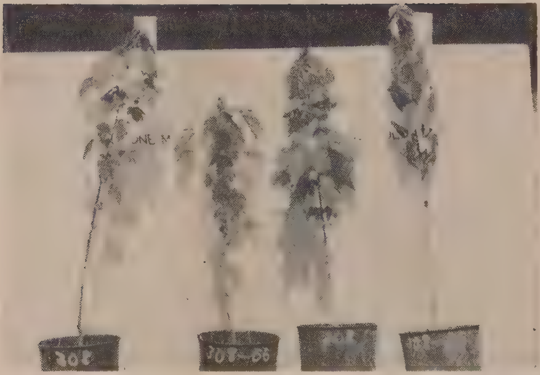

FIG. 4. Chilled and unchilled plants of parentage 308-55 from the Everglades swamp in southern Fla. Plants of this origin had no chilling requirement and there was no apparent difference between the chilled plants on the left and the unchilled plants on the right.

These results indicate a clinal pattern of variation in the requirement for chilling for red maple seedlings from different geographic origins. The differential response to chilling can be correlated with the frost-free seasons that prevail in the native habitats of the experimental plants. In some instances parentages of the same geographic origin vary in their date of break of dormancy in response to chilling treatment (Table I). Not all seedlings from a given plant broke dormancy at the same time, but plants of a given parentage and treatment were arbitrarily classified as growing actively when 80% of the individuals had unfolded their first leaves. Thus, some unchilled plants of parentages 71-54, 72-54, and 73-54 started active growth by April 15, but not until May 15 had 80% of the plants of these parentages started active growth. Some plants of these parentages were still dormant on May 29 when the experimental observations were discontinued. There appears to be genetic variation in winter chilling requirements within as well as between geographic origins of red maple.

One month of chilling treatment was adequate to break the rest requirement of all plants used in this study. All plants broke dormancy and grew normally from 60-80 days after completion of the one month chilling treatment. The plants from Florida broke dormancy from 4-16 days after the completion of the one month chilling treatment.

Plants receiving 2½ months of cold treatment broke dormancy from 25-32 days after completion of the cold treatment. The additional chilling may have caused more prompt initiation of growth by trees from most sources. The conditions of the experiment do not permit a clear-cut decision on this point, since the different chilling treatments are partially confounded by the higher temperatures in the latter part of the spring. Plants from the Everglades broke dormancy within 4 days after completion of the one month chilling treatment. Plants of this same parentage required 17 days to start growth after the 2½ months of chilling treatment. Evidently the effect of the prolonged cold treatment on these plants was to delay their break of dormancy.

Observations on the chilling requirements of different geographic origins of white birch (*Betula papyrifera* Marsh.), yellow birch (*Betula alleghaniensis* Britton) and eastern hemlock (*Tsuga canadensis* L. Carr.) show that these species have similar patterns of genetic variation in their chilling requirements. Detailed reviews of these obsevations will be published.

CORRELATION OF DATE OF BREAK OF DORMANCY WITH GEOGRAPHIC ORIGIN AND VARIOUS TEMPERATURE FACTORS

An attempt was made to correlate the date of the break of dormancy of the various geographic origins of red maple with the variations in climate over the range of the species. Figure 5 shows the correlation between the date of break of dormancy of the plants used in this study and the frost-free season. Figure 6 shows the linear and quadratic relationship between the date of break of dormancy for the plants and the July average temperature. A quadratic function (see the following paragraphs) gives significantly better correlation. The climatic data used in preparing the figures and the subsequent calculations were obtained from the 1941 Yearbook of Agriculture, "Climate and Man."

Because of the importance to forest planting programs, researchers have attempted to correlate plant behavior

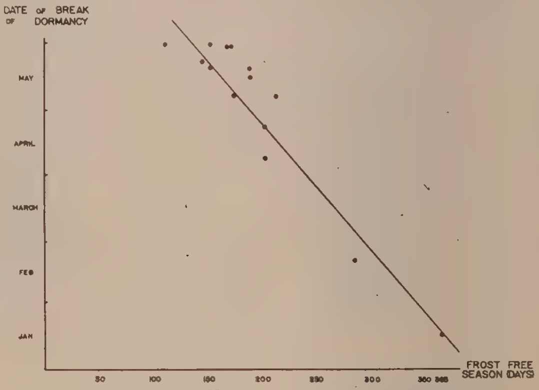

FIG. 5. Correlation of date of break of dormancy with the frost-free season for the different geographic origins of red maple used in this study. (r = 0.96 on 24 degrees of freedom). Some plotted points represent more than one observation.

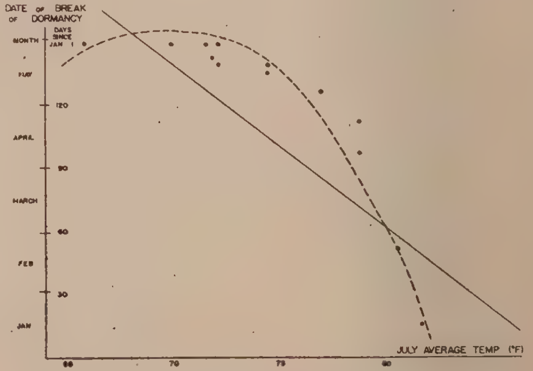

FIG. 6. Graph of the linear and quadratic relationships between date of break of dormancy for plants used in this study and the July average temperature. The quadratic relationship (dashed line) gives a significantly better correlation. r = 0.85 for linear correlation. r = 0.95 for quadratic correlation. Some plotted points represent more than one observation.

with various temperature factors, such as July average temperature, January average temperature, January maximum or minimum temperatures, July maximum or minimum temperatures, etc. (Daubenmire 1959, Langlet 1959, Rudolf 1957, Kriebel 1956, 1957, Olsen et al. 1959). One recent attempt has been made to correlate plant growth with the number of degree hours above an arbitrary temperature that prevails during a given portion of the growing season (Brown 1953). (Degree hours = degrees above an arbitrary minimum x the number of hours that the temperature prevails). Actually all these factors are strongly correlated; hence various phenological and growth data can be correlated with any one or a combination of several of these temperature and heat measurements. Some indication of the relationship amongst the various temperature measures is revealed by pairing them off and calculating their correlation coefficients. This was done for the geographic locales represented by the red maple collections used in this study: July average temperature and frost-free season are highly correlated ($r = 0.88$ on eight degrees of freedom); January average temperature and frost-free season are highly correlated ($r = 0.97$ on 8 degrees of freedom); January average temperature and July average temperature are highly correlated ($r = 0.85$ on 8 degrees of freedom). The statistical department of the University of Florida ran correlation analyses on the date of break of dormany (Y = days after January 1) with the frost-free season (X_1) and the July average temperature (X_2). Some of the regression equations they obtained are given below:

The total variance of $Y = 68744.6$

1. $\hat{Y} = 232 - 0.600X_1$
$\Sigma (\hat{Y} - Y)^2 = 2897, \; r = 0.96$
2. $\hat{Y} = 679 - 7.69X_2$
$\Sigma (\hat{Y} - Y)^2 = 106435, \; r = .85$
3. $\hat{Y} = -4602 + 136.559X_2 - 0.9784X_2{}^2$
$\Sigma (\hat{Y} - Y)^2 = 3339, \; r = 0.95$
4. $\hat{Y} = 163.428 - 0.663X_1 + 1.096X_2$
$\Sigma (Y - Y)^2 = 3922, \; r = 0.94$
5. $\hat{Y} = -248.86 + 4.958X_1 + 4.905X_2 - 0.0653X_1X_2$
$\Sigma (\hat{Y} - Y)^2 = 814, \; r = 0.98$

All regression coefficients in these equations are significant at the 1% level of confidence.

Note that even the quadratic function of July average temperature (equation 3) does not give as good a correlation with the date of break of dormancy for the red maple origins as does the frost-free season (equation 1). The regression of date of break of dormancy on frost-free season and July average temperature (equation 4) gives a poorer correlation than the frost-free season alone (equation 1). Only when the interaction term for July average temperature and frost-free season is included in the regression analysis (equation 5) does the correlation improve over equation I. As noted before, the correlation between January average temperature and frost-free season for the localities included in this study is 0.85. Therefore, January average temperature could be substituted for X_2 in equation 5, and a significant relationship would still result.

The results indicate that when only one temperature factor is considered in assessing the limits of safe movement for seed from its place of origin to a foreign place for planting the frost-free season is the simplest and most accurate measurement. The use of additional temperature measurements such as July average temperature will increase the reliability of the necessarily arbitrary limit of safe transplantation for various tree species.

SUMMARY

Seedlings from different geographic origins in the range of red maple (*Acer rubrum* L.) were subjected to various chilling treatments. The contrasting time and manner of break of dormancy by the chilled and unchilled plants of different geographic origins indicate both racial and local variations in the chilling requirement of red maple. Plants from extremely cold portions of the range of red maple do not break dormancy without adequate chilling, while plants from the Everglades region of Florida have no chilling requirement.

Analyses of the correlations between the various temperature factors and the date of break of dormancy for different origins of red maple are presented. The results reveal a strong correlation among July average temperature, January average temperature, frost-free season, and other temperature factors. The best prediction of date of break of dormancy was obtained when July average temperature and frost-free season and their interaction term were considered. Where only one temperature measure is used, frost-free season gives the best correlation for date of break of dormancy. The significance of these results for tree planting programs is discussed.

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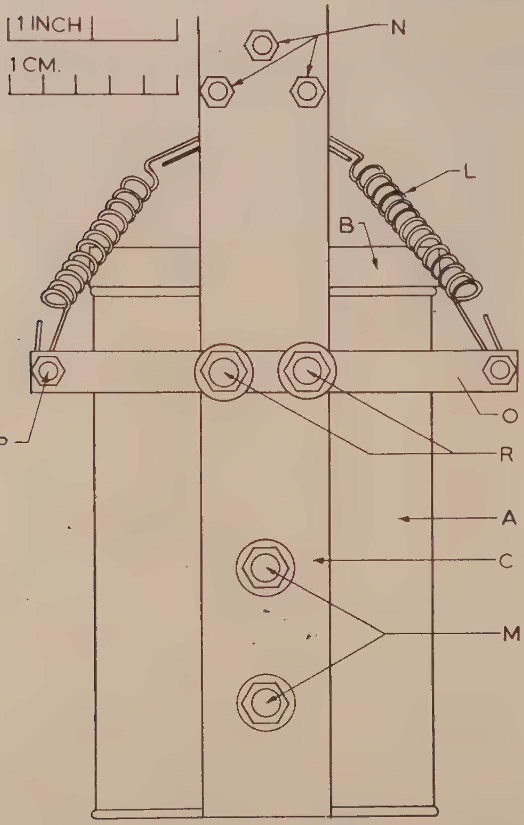
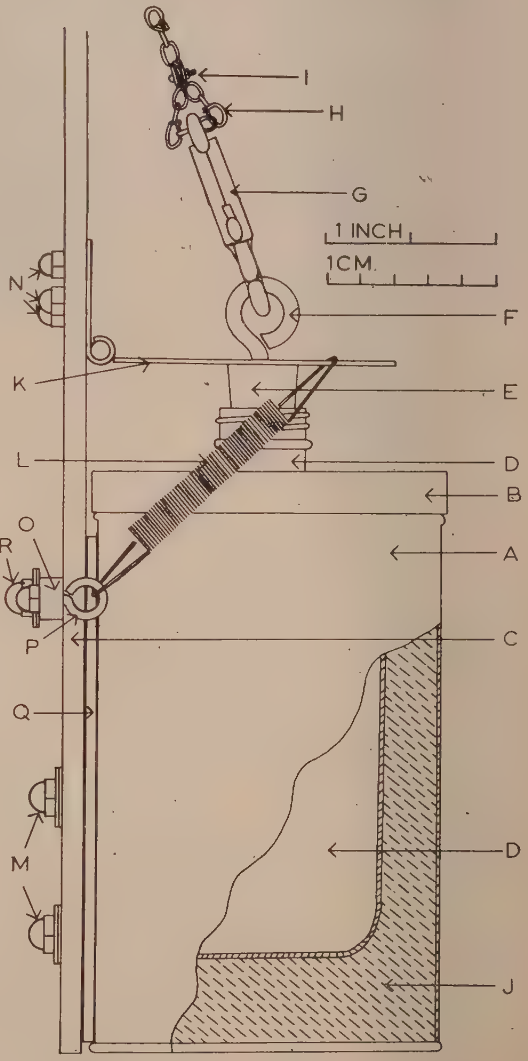
A NEWLY DESIGNED APPARATUS FOR WATER SAMPLING AT SHALLOW DEPTHS[1]

At the beginning of a bacteriological survey of the waters of Pymatuning Lake undertaken in 1950, the only water sampler available was a Kemmerer model (Foerst modification). For the purposes of the contemplated investigation, this apparatus was unsatisfactory because the study would require a large number of water samples,





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[1] Publication No. 23 of the Pymatuning Laboratory of Field Biology of the University of Pittsburgh.

each to be stored in a sterile container for subsequent laboratory analysis.

A survey of the literature dealing with water samplers showed that Wilson (1920) had discussed water samplers used by other researchers up to that time. All these samplers, along with the Hale and the Irwin samplers described by Welch (1948), were rejected as too complicated. Mortimer (1940) devised a very good sampler for use in deep water; its use in a shallow lake, however, would entail a great deal of wasted effort.

It was therefore considered desirable to design and build a sampler to meet the specific needs of the proposed work. The requirements were that it be inexpensive, effective, simple to construct, and that it permit sterilization of parts where necessary.

A sampler devised to meet these requirements was constructed as shown in Figures 1-4. Parts referred to in subsequent descriptions of the apparatus are listed alphabetically on the legend accompanying the figures, with dimensions, sizes, or other identification of each part.

One end of an aluminum bar (C) was attached by 2 round-head brass machine screws (M) and nickel-plated brass cap nuts to the outside of a wide-mouthed, round metal can (A). One large, flat brass washer was used inside the can and 2 outside with the cap nut. Between the can and the long aluminum bar was placed a shim consisting of another aluminum bar (Q). This permitted the lid (B) to be screwed on and off.

An aluminum cross bar (O) was centered perpendicular to the long aluminum bar (C) with its lower edge 5⅛ in. from the bottom of the can. This cross bar was held in place by 2 brass round-head machine screws and nickel-plated brass cap nuts (R). Three large, flat brass washers were used, one inside the can and 2 next to the nut. The cross bar was placed with the ¼ in. side horizontal and the ½ in. side vertical. A cadmium-plated eye bolt (P) was placed ¼ in. from each end of the cross bar and attached with a nickel-plated brass cap nut. These eye bolts were situated on the side of the bar nearest the can.

A safety hasp (K) was placed on the inside of the long bar next to the can, 9⅝ in. from the bottom of the handle. It was attached to the handle by 3 flat-head brass machine screws and nickel-plated brass cap nuts (N).

The safety hasp (K) as purchased contained a slot ¼ x ⅛ in. which was centered ⅞ in. from the long end of the hasp. A second slot of the same size was cut in the safety hasp and centered 1¾ in. from the long end of the hasp.

The bottle used in the sampler was a Boston Round pint bottle (D) made of Duraglas. The bottle was fitted with an Escher-type rubber stopper (E), size No. 2. A No. 105 screw eye (F) was screwed down into the center of the top of the Escher stopper.

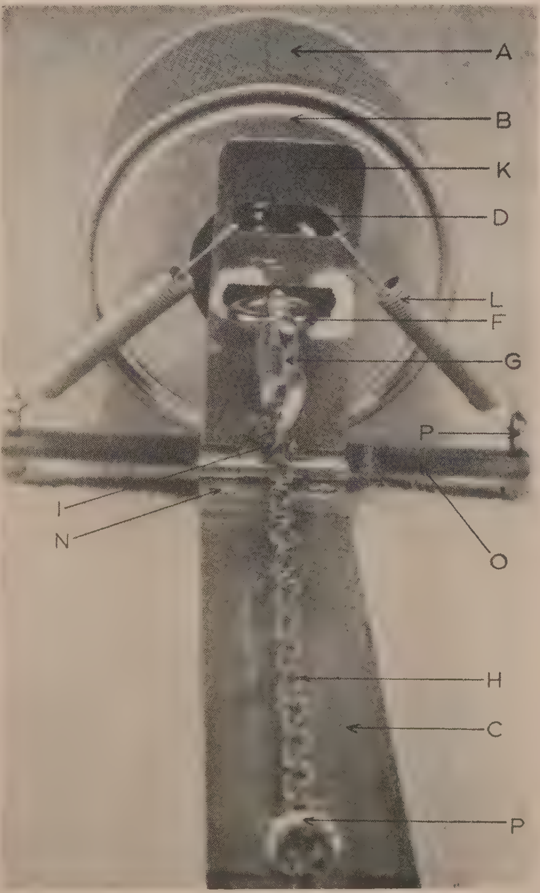
When the sampler had been assembled thus far, it was held in a vertical position by a burette clamp attached to an apparatus support stand. The screw-top lid was removed from the can, and a circular hole 1¾ in. in diameter was cut in the center of the lid.

The bottle with the Escher stopper and screw eye was placed inside the can. The screw eye was raised up through the innermost slot in the safety hasp until the hasp rested on the Escher stopper. With the stopper firmly seated in the bottle, it was raised until the safety hasp was perpendicular to the handle. At this point the neck of the bottle was secured in place by a burette clamp attached to another apparatus support stand.

Next, approximately 1¼ lbs. of paraffin were melted and poured into the sampler between the bottle and the can to within ½ in. of the top of the can. After the paraffin had solidified, the burette clamp was removed from the neck of the bottle. Then the safety hasp was raised and the Escher stopper removed. The bottle was filled with boiling water and was easily freed from the paraffin by a spinning motion. The melted paraffin adjacent to the bottle then resolidified. Thus a support mold of paraffin was fashioned to hold the sample bottle at the proper level inside the sampler.

One ft from the lip of the sample bottle an eye bolt and nut (P) were attached to the center of the long aluminum handle. The eye was placed with the open area perpendicular to the base of the sampler. Five more such eye bolts were fixed at one ft intervals on up the handle of the sampler. An additional eye bolt was attached at a point 2 m from the lip of the sample bottle at the very top of the handle.

To the eye bolt at the 2 m mark was attached 82 in. of No. 5 Tenso chain (H). The chain was threaded through the eye bolt and a loop formed. A round-head brass machine screw, hex nut and 2 washers (I) were slipped through this loop to secure the chain. The remainder of the chain was passed through the eye bolts



down the handle. At the end of the chain was attached a cadmium-plated snap clamp (G) by the same type of bolt (I) used at the top of the chain. The snap clamp gripped the screw eye in the Escher stopper.

When the chain was raised, it lifted the Escher stopper out of the bottle. To replace the stopper in the bottle, a pair of 4 in. tension springs (L) were attached through the outermost slot in the safety hasp to each of the eye bolts on the ends of the cross bar.

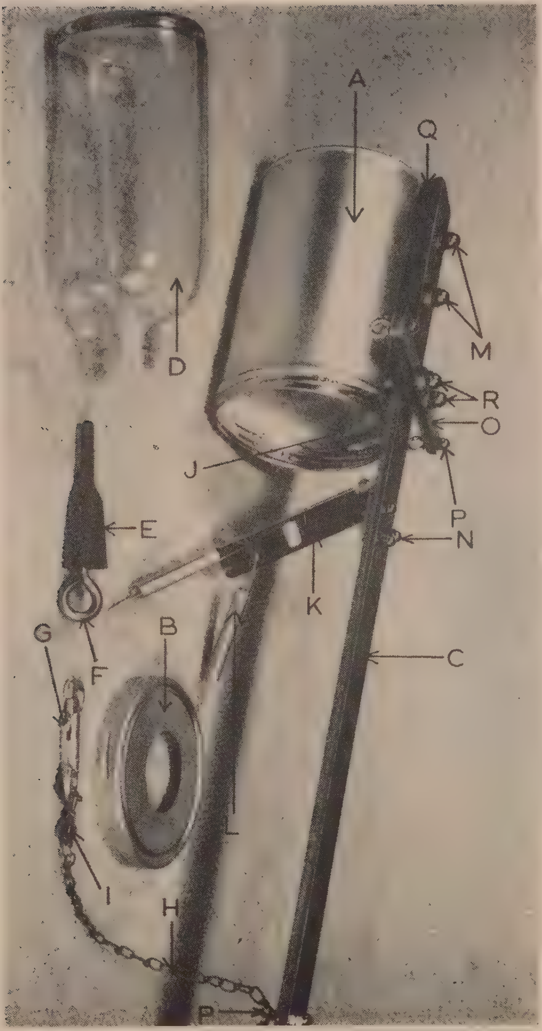
The operation of the sampler in the field is very simple. The researcher should be provided with a sufficient supply of sterile sample bottles fitted with Escher stoppers and eye bolts. The screw-top lid of the can is removed, the safety hasp raised, and a sterile sample bottle is placed in the sampler in such a way that the eye bolt in the Escher stopper will pass through the innermost slot in the safety hasp. The lid is then screwed onto the can, and the safety hasp is lowered over the eye bolt. The eye bolt should then be turned until it is perpendicular to the slot in the safety hasp. The snap clamp is next hooked through the eye bolt.

To collect the sample, the sampler is lowered to the proper depth as indicated on the handle of the sampler. The chain is raised about one in., which is sufficient to open the sample bottle. After allowing enough time for the sample bottle to fill, the chain is released. The 2 tension springs attached to the safety hasp cause it to apply enough pressure against the Escher stopper to reseat it securely in the sample bottle. The sampler is then raised. The snap clamp is removed from the eye bolt, the eye bolt is turned enough to permit raising the safety hasp, and the filled bottle is removed from the sampler. This procedure is followed for succeeding samples, a fresh sample bottle being used for each.

The parts used in building the sampler were selected for their simplicity and the ease with which they might be obtained. The tools employed in its construction may be hand tools, although power tools make the task easier. Some modifications in various parts will not alter the operation of the sampler. Ordinary sash cord may be substituted for the Tenso chain. It is not as durable as the chain, but if the sash cord breaks, only a few parts will be lost. Brass sash chain may also be substituted for the Tenso chain. In our own experience it has been found that ⅛ in. nylon-covered tiller rope can be substituted for the Tenso chain with good results. Tiller rope clamps and thimbles are then used to attach the rope.

Bottles of heat-resistant glass may be substituted for the Duraglas bottles, but this will increase the cost of the apparatus. Bottles of other sizes may also be substituted for the pint bottles when the paraffin mold is being made.

If the sampler is to be used in an area where the temperature is above 30°C, the paraffin may be replaced



Figs. 1-4. Scale drawings and photographs depicting a newly designed apparatus for water sampling.

(A)—Screw-top Can, No. 30 American Can Co., 6⅝ in. x 4 in. dia. (Difco-Agar Can) sprayed with aluminum paint.

(B)—Lid of screw-top can, 4 in. dia.

(C)—Aluminum bar, 86½ in. x 1½ in. x ¼ in.

(D)—Boston Round pint bottle, Duraglas, 6½ in. x 2⅞ in.

(E)—Escher stopper, rubber, No. 2 size, 2⅞ in.

(F)—No. 105 Screw eye, 2 in.

(G)—Snap clamp, cadmium-plated, 2½ in.

(H)—Tenso chain, No. 5, or Brown chain, 82 in.

(I)—Round-head brass machine screw, 4 x 40 x ½ in., hex nut, and 2 washers.

(J)—Paraffin, 1¼ lb.

(K)—Safety hasp, 3½ in. x 1½ in.

(L)—Tension springs, 4 in., (No. 61, Admiral Spring Mfg. Co., N. Y. 3, N. Y.)

(M)—Round-head brass machine screw, ¼ in. x 20 x ¾ in., 3 large ¼ in. brass washers, and nickel-plated brass cap nut.

(N)—Flat-head brass machine screw, 8 x 32 x ½ in., and nickel-plated brass cap nut.

(O)—Aluminum bar, 6 in. x ½ in. x ¼ in.

(P)—Cadmium-plated eye bolt, 8 x 32 x 1⅝ in. (cut down to ⅞ in.) and nickel-plated brass cap nut.

(Q)—Aluminum bar, 5½ in. x 1½ in. x ⅛ in.

(R)—Round-head brass machine screws, ¼ in. x 20 x 1 in., large ¼ in. brass washers, and nickel-plated brass cap nuts.

by a resinous sealing wax which is satisfactory up to 90°C.

Although this sampler was designed primarily for use in bodies of water to 2 m in depth, it is suitable for several other applications. It might be convenient for collecting samples from various stages in water or sewage treatment plants. It could also prove useful for industrial processes, such as vat and tank sampling.

A similar sampler could be built by almost anyone. All its parts are easily obtainable, and its construction does not require special mechanical tools or skills. It is inexpensive enough not to strain a limited budget; the total cost for parts was less than $8. It has, moreover, been used successfully for more than a year without developing operational flaws.

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EFFECTS OF TEMPERATURE UPON PHOTOSYNTHESIS AND RESPIRATION OF CHOCTAWHATCHEE SAND PINE[1]

MATERIALS AND METHODS

One-year-old seedlings of sand pine grown in Calhoun County, Fla. were used in this study. Seedlings received in December, 1958, were potted in metal containers, treated biweekly with a complete fertilizer, watered, and grown under normal day conditions in a greenhouse in Durham, N. C. Temperature in the greenhouse averaged about 24° C, with a high of 37° C on hot days and a low of about 13° C during cool nights.

After 13 weeks of growth, 6 seedlings were selected for testing on the basis of good vigor and uniformity of size. A single seedling was subjected to the entire range of temperatures, 18 to 48° C at 5° intervals, for one day. Each seedling was watered to field capacity the day before it was studied.

Rates of photosynthesis and respiration were calculated from the length of time needed for seedlings to either remove or add CO_2 to a closed system. Time measurements were taken between CO_2 levels of 5% above and 5% below normal air concentration (300 ppm). The rates of photosynthesis and respiration were expressed in mg of CO_2 per plant per hour.

Before analysis, each seedling was conditioned for at least 20 min at each temperature. Intensity of the light source (4,000 ft-c at the middle of the seedling) remained constant in all tests. At least 3 measurements of photosythesis and two of respiration were made on each plant at each temperature before it was subjected to a higher temperature. The desirability of varying this regimen is acknowledged, but length of time needed for such variation made it impractical. Respiration measurements were made 20 min after photosynthesis measurements at each temperature. Seedlings were watered when necessary during the tests. The measurements on all 6 seedlings were completed within 7 days during April, 1959.

Exchange of CO_2 was measured with a Grubb-Parsons Infra-Red Gas Analyzer, as described by McGregor (1958). The equipment used in conjunction with the gas analyzer was the same as that described by Decker (1944), with certain modifications. Each seedling was placed in a cellulose acetate chamber located in a controlled temperature cabinet under a bank of high intensity lights. Water, circulated in a layer over the chamber, absorbed much of the heat from the light source. Chamber temperatures were further controlled by a water refrigeration system, while air was circulated through the analyzer and chamber by a small vacuum pump and mixed in the chamber by a small fan.

Average rates of apparent photosynthesis and respiration in the dark were determined at selected temperatures ranging from 18°-48° C. Actual photosynthesis was calculated by totaling the values attributable to apparent photosynthesis and respiration in the dark. Immediately after the completion of each run all needles were stripped from the seedlings and weighed. Needle length in centimeters was then measured, after which the needles were oven dried to constant weight at 105° C for dry weight measurements.

An analysis of variance was used to determine whether differences in rates of CO_2 exchange due to varying temperatures were statistically significant. Also, statistical analyses were made to indicate which of the 3 indices of measurement (needle fresh weight, dry weight, and length) was the most suitable expression for CO_2 exchange.

RESULTS AND DISCUSSION

The average rates of respiration, apparent photosynthesis, and actual photosynthesis for each of the 3 indices of needle measurement are in Table I.

Since each CO_2 exchange rate value can be given equal statistical weight, and since measurements were taken at equal temperature intervals, the Fisher and

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[1] Sand pine (*Pinus clausa* (Chap.) Vasey) is of interest because of the temperature extremes to which it is subject during the period of establishment. This paper reports studies of apparent photosynthesis and respiration over a range of temperatures for the Choctawhatchee race of this species. The rates of photosynthesis are compared with those of loblolly pine, measured in previous studies by Decker (1944) and McGregor (1958). These comparisons are of interest because the ranges of the species overlap.

TABLE I. *Rates of photosynthesis and respiration at various temperatures* (as mg of CO_2 exchanged per hour)*

Temperature (°C)	Apparent Photosynthesis			Actual Photosynthesis			Apparent Respiration		
	per g of fresh needle weight	per g of dry needle weight	1,000 cm needle length	per g of fresh needle weight	per g of dry needle weight	1,000 cm needle length	per g of fresh needle weight	per g of dry needle weight	1,000 cm needle length
18	4.7	15.8	11.0	5.0	16.9	11.8	0.3	1.1	0.8
23	5.7	19.2	13.4	6.3	21.3	14.9	0.6	2.1	1.5
28	5.4	18.4	12.8	6.3	21.4	14.9	0.9	3.0	2.1
33	4.8	16.2	11.4	6.0	20.5	14.3	1.3	4.3	3.0
38	3.6	12.3	8.6	5.8	19.1	13.3	2.0	6.8	4.7
43	1.7	5.7	4.1	3.8	13.1	9.2	2.2	7.3	5.1
48**	−1.6	−5.5	−3.8	0.8	2.8	2.0	2.4	8.3	5.8

* Each value is the average of measurements obtained from 6 seedlings.
** Compensation had been reached for apparent photosynthesis.

Yates (1949) method of fitting orthogonal polynomials was used to calculate a regression equation. Where Y is considered to be the CO_2 exchange rate and X is the temperature, then the equation to be fitted is of the form

$$Y = \alpha + bS_1 + cS_2 + dS_3$$

where the S's are polynomial functions in X, and are given in the Fisher and Yates' tables.

An analysis of variance for individual contributions of S_1, S_2, etc. on rates of photosynthesis (apparent and actual) and resipration was used for each of the 3 indices. It was clear from these analyses that a polynomial of the second degree would produce an acceptable regression equation when Y was expressed in logarithmic form.

An attempt was then made to determine which index of needle measurement had the least mean squares of residuals independent of temperature. An analysis of variance for respiration, based upon common, general, and group regressions disclosed a significant difference (1% level) between plant means, but no difference among plant regressions. The difference between plant means is probably due to the natural variation between seedlings. The general regression on temperature was highly significant (1% level).

However, there was no significant difference between the mean squares of residuals for rate of respiration on a fresh weight, dry weight, and length basis. The regression equations for respiration, with Y as the rate of respiration per unit of needle measurement, were as follows:

Fresh Weight (per gm)—
$\text{Log } Y = 0.4330 + 0.14659S_1 - 0.01932S_2$
Dry Weight (per gm)—
$\text{Log } Y = 0.57331 + 0.14658S_1 - 0.01931S_2$
Needle Length (per 1,000 cm)—
$\text{Log } Y = 0.41756 + 0.14659S_1 - 0.01932S_2$

The high agreement between these equations indicates that the simplest method of measurement can be used with confidence.

Of special interest is the tendency for the respiration rate to increase in a straight-line relationship up to a temperature of 33° C, to rise rapidly between temperatures of 33° and 38° C, to remain constant between 38° and 43° C, and to rise again at 48° C. Even though differences in the rate of respiration between 38°-43° C and 43°-48° C were not significant, the difference in rate between 38° to 48° C was significant, and thus confirms this upward trend.

Rate of apparent photosynthesis was maximum near 23° C, and reached its compensation point between 43° and 48° C. Within this range of temperatures, the rate of respiration in the dark was at its highest level and probably contributed heavily to the decrease in rate of apparent photosynthesis. Actual photosynthesis was calculated by summing the values of respiration in the dark and apparent photosynthesis. However, there is evidence that respiration in the dark is not the same as respiration in the light during photosynthesis. An outburst of CO_2 was noted by Decker (1955, 1957) immediately after illumination was extinguished. This phenomenon occurred with white ash, yellow poplar, and with several other species. If this took place during the study, actual photosynthesis rates may be higher than those shown in Table I. The maximum rate of actual photosynthesis occurred between temperatures of 23° and 28° C.

At temperatures above 40° C, needles which were one to 3 months old showed signs of a water deficit even though soil moisture was adequate. However, needles less than 10 days old showed no symptoms of a water deficit at these temperatures. This seems to confirm the apparent water priority of rapidly growing tissues under conditions of high moisture stress.

Results of this study on sand pines are similar to those obtained from one-year old loblolly pine by McGregor (1958). However, they differ from those obtained by Decker (1944) using two-year old loblolly pines. Decker found that the rate of apparent photosynthesis was slightly higher at 30° C than at 20° C, when measured under 4,500 ft-c of light. McGregor's apparent photosynthesis rates are given in mg of CO_2/1,000 cm of fascicle length. When these rates are divided by 3 to place them on a 1,000 cm needle length basis and are then compared with sand pine rates at various temperatures, it is found that sand pine has a slightly higher rate of apparent photosynthesis (1-2 mg of CO_2/1,000 cm of needle length) than loblolly pine at most temperatures. However, loblolly pine measurements by McGregor were made in July, whereas the sand pine was measured in April. McGregor found that seasonal maximum rate of apparent photosynthesis for loblolly pine occurred in July and August. If this seasonal maximum holds for sand pine, then its rate of apparent photosynthesis may be 10-20% higher in July than in April.

The relative efficiency of sand pine in carrying on photosynthesis at higher temperatures may explain its success of establishment on the hot sands of Florida. Such amplitude apparently does not extend to other species of pine which may grow in the immediate vicinity, but in differing habitats.

ACKNOWLEDGMENTS

The authors wish to thank Dr. W. H. Davis McGregor, Dr. F. X. Schumacher and Dr. P. J. Kramer for their advice concerning this project. They also wish to thank the Southern Forest Experiment Station, Marianna, Florida for furnishing plant material.

SUMMARY

(1) Rates of photosynthesis and respiration in the dark were measured using seedlings of the Choctawhatchee race of sand pine (*Pinus clausa*. Chapm. Vasey). Temperatures were varied from 18°-48° C, while light intensity remained constant at 4,000 ft-c.

(2) The rate of apparent photosynthesis was at a maximum near 23° C and became negligible between 43°-48° C.

(3) Respiration in the dark reached a maximum at 48° C, the highest temperature used.

(4) It was shown by statistical analysis that needle fresh weight, dry weight, and length may be used with equal confidence as a basis for expressing rates of CO_2 exchange.

(5) Although the results indicate that sand pine seedlings may be more efficient photosynthetically than loblolly pine, more exacting comparative work is necessary to confirm this apparent trend.

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DISTRIBUTION OF PONDEROSA PINE DWARF MISTLETOE IN THE VICINITY OF AN ARIZONA VOLCANO[1]

The scarcity of dwarf mistletoe (*Arceuthobium vaginatum* f. *cryptopodum* (Engelm.) Gill) in the ponderosa pine (*Pinus ponderosa* Laws.) stands in the volcanic cinder area northeast of Flagstaff, Arizona, is well known (Korstian and Long 1922, Pearson 1950). However, little is known of the detailed distribution of the parasite in this area.

This cinder area is associated with Sunset Crater, the most recent volcano in the San Francisco Mountain volcanic field (Robinson 1913, Colton 1932). Estimates based on dendrochronological and archaeological data suggest that it erupted between 1046 and 1071 A. D., probably in 1067 (Colton 1945). The distribution of ash from the eruption is shown in Figure 1, which was adapted from a map published by Colton (1932). An inner (the lapilli) zone covers about 100 sq. miles, most of which is in the ponderosa pine type. This zone is characterized by large cinder particles ¼ to one inch in diameter. The outer (black ash dune) zone covers about 700 sq. miles and consists of smaller ash particles. This zone is oval-shaped with the long axis north and south. It extends about 6 miles to the west of the crater and about 22 miles to the east. Only about one-tenth of the black ash dune zone supports ponderosa pine because most of it is below 6,000 ft. elevation, where pinyon-juniper or grassland types prevail.

Korstian and Long (1922) state that dwarf mistletoe infection is rare on these cinder areas and is light where it does occur. Pearson (1950, p. 51) states that no mistletoe is present on a 320 acre permanent plot located about 6 miles south of Sunset Crater in the black ash dune zone (Fig. 1). He also reports that the growth rate of individual trees in the cinder area is about the same as on the other ponderosa pine sites in the vicinity but that the stands are typically open and have lower per-acre volumes.

METHODS

Observations from a slow-moving vehicle were made to detect the occurrence of dwarf mistletoe in ponderosa pine. The traveled roads were chosen impartially and observation transects 1 chain (20.12 m) wide on both sides were used. The sampled area was thus 16 acres per linear mile of road traveled. Locations of the traveled roads are in Figure 1.

RESULTS

The results of the roadside reconnaissance are summarized in Table I. A total of 76.7 miles of road in the ponderosa pine type was traveled. The observed stands totaled 1,227 acres, or approximately 2% of the ponderosa pine acreage in this area. Stands with dwarf mistletoe composed only 0.8% of the forested area (Table I). The only infected stands found in the cinder area were on the western limits of the black ash dune zone

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[1] Acknowledgments are expressed to Harold S. Colton and W. B. McDougall of the Museum of Northern Arizona, Flagstaff, for information on the geology and botany of the Sunset Crater area and also for reviewing the manuscript. The research herein reported was conducted at the Forest Disease Laboratory, Albuquerque, N. M.

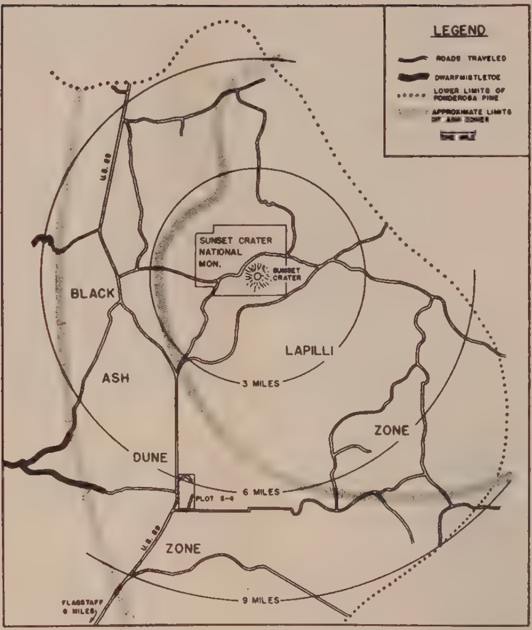

Fig. 1. Map of Sunset Crater and vicinity where ponderosa pine stands were examined for dwarf mistletoe. Approximate limits of the lapilli and black ash dune zones and the lower limits of ponderosa pine are from Colton (1932).

(Fig. 1). The nearest infected stands were about 6 miles west of Sunset Crater just outside the black ash dune zone. No infection was found in ponderosa pine in the lapilli zone.

Table I. Distribution of dwarf mistletoe within the Sunset Crater ash zones

	Lapilli Zone		Black Ash Dune Zone		Totals	
Distance from crater	Stands examined	Dwarf mistletoe	Stands examined	Dwarf mistletoe	Stands examined	Dwarf mistletoe
Miles	*Miles*	*Per cent*	*Miles*	*Per cent*	*Miles*	*Per cent*
0-3........	20.1	0	—	—	20.1	0
3-6........	17.7	0	17.9	0	35.6	0
6-9........	4.4	0	16.6	3.6	21.0	2.9
Totals or averages....	42.2	0	34.5	1.7	76.7	0.8

The area in which the ponderosa pine forest was killed by the eruption is not known, but it seems likely that most stands within the lapilli zone were destroyed. Colton (1932) suggests that ponderosa pine now extends farther to the east than before the eruption of Sunset Crater. His hypothesis is based on the fact that ponderosa pine extends nearly 1,000 ft. lower in elevation in the Sunset Crater cinder area than on adjacent soils. Thus, stands on a large part of the cinder area appear to have developed since the eruption, or within the last 900 yr.

The absence of dwarf mistletoe in ponderosa pine on the cinder area, except along its western edge, may be due primarily to the slow rate of invasion of the parasite into this area from heavily infected stands to the west. Dwarf mistletoe on this adjacent area was found on 37% of the ponderosa pine acreage. These stands are also on volcanic soils, but the volcanic activity is several thousand years old (Colton 1950).

Recent work[2] indicates that this dwarf mistletoe spreads at the rate of 1 to 2 ft. per year. This study tends to confirm a slow spread. However, it is impossible to estimate the rate of spread from the Sunset Crater data because neither the limits of original stand destruction nor the period that new forests have been established is known.

Infection centers within the cinder area have been reported (Korstian and Long 1922), but none were found in this study, despite the examination of 70 miles of roadside stands plus additional searches on foot. Isolated infection centers are to be expected, as they are found occasionally in other southwestern ponderosa pine stands. The vectors responsible for the establishment of isolated centers are not known, but presumably birds are involved. Although infection centers probably exist in the cinder area, this study suggests that they would account for an exceedingly small proportion of this ponderosa pine stand.

Summary

The ponderosa pine stands in the cinder area near Sunset Crater, Arizona, were examined for dwarf mistletoe, *Arceuthobium vaginatum* f. *cryptopodum*. This volcano erupted about 900 yr. ago, and most of the ponderosa pine stands here have developed since the eruption. Stands with dwarf mistletoe constituted only about one per cent of this area and were limited to its western edge adjacent to heavily infected ponderosa pine on older volcanic soils. On the adjacent area 37% of the ponderosa pine acreage was infected.

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[2] Manuscript by F. G. Hawksworth entitled "Dwarfmistletoe of ponderosa pine in the Southwest" being processed for a U. S. Department of Agriculture Technical Bulletin.

A LOW-COST CONTROLLED ENVIRONMENT CABINET WITH DIURNAL TEMPERATURE FLUCTUATION[1]

F. W. Went (1943, 1950, 1957) has demonstrated at the California Institute of Technology the practicability of precise environmental control for plant research. That the need for controlled environments is not new can be realized from some of the early papers reviewed by Parker (1944). The large amount of research reported since Went's publications indicates the value of the control of the plant's environment in the eyes of the plant scientist, particularly in the fields of ecology, genetics and physiology.

Unfortunately, installation of equipment on a scale in use at the California Institute of Technology is denied many institutions because it entails not only a tremendous capital cost but also expensive maintenance. Went (1957) gives the cost of the phytotron to be $422,422.40.

In order to conduct research on a more modest budget and at the same time provide for certain versatility, smaller installations consisting of rooms or cabinets have been described incorporating controls of various elements of the environment. Parker (1944) has reviewed much of the earlier literature on the construction of these units. Hoyman (1955) has described an installation used for inoculation studies. He utilized daylight illumination and made provision for humidification and lowered temperatures. Mitchell (1950) described a cabinet with artificial illumination. Platt (1957) has written of a cabinet with high light intensity using artificial light. Several growth rooms and growth cabinets have been described by different authors (Hudson 1957 a, b). Hudson has clearly differentiated among the three types of installations, the phytotron, the room, and the cabinet. The cabinet described by Chapman (1956) was designed with economy of construction in mind. His unit provides for artificial illumination, and temperature and carbon dioxide control, but not humidity control.

The present paper describes a controlled environment cabinet of moderate cost. Features of the equipment are temperature control on a diurnal fluctuating basis, control of length of day, and partial control of relative humidity. In order to reduce expense, commercially available rather than custom designed materials were used throughout.

The basic unit was a 75 cubic foot five-door reach-in refrigerator (Fig. 1). This unit provided the insulated box as well as the refrigeration and air circulation systems. These are the major items of expense in a controlled environment cabinet. To complete the cabinet, it was necessary to add timing devices, lights, humidity control, and a system for a diurnal change in temperature.

The materials used were predicated upon the size and other characteristics of the one major item of expense, the refrigerator. Since such an item may be available in somewhat different dimensions and other particulars, it may not be possible for others interested in building such a cabinet to use the specific items used in the present installation. A list of items used is nevertheless included at the end of the paper. Costs of individual items are not included because prices will vary from place to place and from time to time—particularly the refrigerator. A brief check of the parts list at the end of the paper by refrigerator and lighting supply companies will give a more meaningful estimate of the costs of the cabinet for a specific installation than any figures supplied by the authors. Costs of material and equipment but not including labor were in the present instance less than $250.00 a unit.

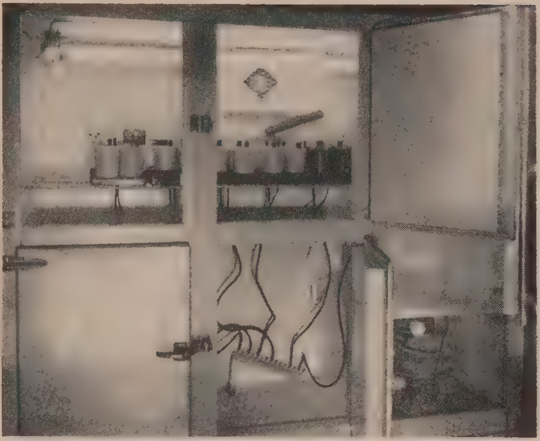

Fig. 1. Low cost controlled environment cabinet constructed with diurnal temperature control, day length control, and partial control of relative humidity. Air circulation fan with sliding covers at upper center. Tubes from drip pans to manifold lower center. The original compressor unit is shown at lower right.

Lighting

Lighting was provided by a bank of eight instant start fluorescent tubes (Fig. 1). These were equipped with ballasts designed for lamps one size larger. Ballasts were mounted outside so that heat produced from them would not be liberated into the box. In addition, four incandescent lamps were provided in a ratio of 1 to 4 watts as recommended by Ditchman (1955). Day length was controlled by an automatic time switch situated at the rear of the unit. The interior of the box was sprayed with white gloss enamel in order to give maximum reflectance. The effect of the enamel is shown

Table I. Effect of High-gloss Enamel on Light Intensity* in a Cabinet

Distance of meter from lights (inches)	Distance from side wall (inches)	Unpainted aluminum surface (ft. candles)	High-gloss enamel surface (ft. candles)	Increase due to painting (%)
Meter 10" from level of lights	2	460	1030	124
	22	1095	2380	117
Meter 20" from level of lights	2	460	1300	182
	22	746	1900	158
Meter 30" from level of lights	2	412	1140	178
	22	570	1560	174

* Light source was a solid bank of fluorescent tubes the full width of cabinet

in Table I, which gives the amount of light in a painted box compared with an unpainted one with aluminum metal walls.

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[1] Published with the approval of the Director of the University of Hawaii Agricultural Experiment Station as Technical Paper No. 455.

TEMPERATURE CONTROLS

It has been shown that diurnal temperature change is essential for vigor in peas (Highkin 1958) and other plants (Went 1957). An important feature of the cabinet, therefore, was provision for diurnal fluctuation of temperature. The essential feature of the two-control system was a time switch which would automatically cut one of the temperature controls in or out of the circuit, as shown in the wiring diagram of Figure 2.

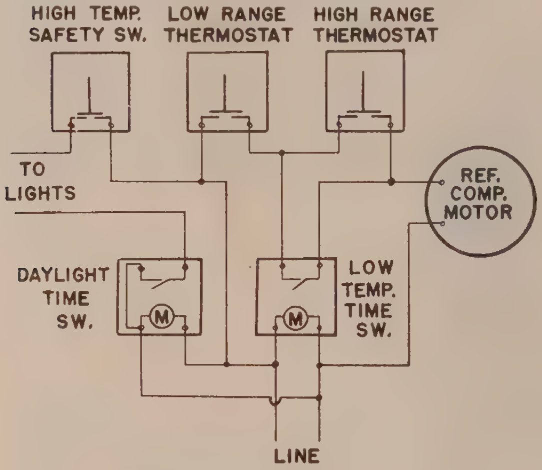

FIG. 2. Wiring diagram for diurnal control of temperature and light in controlled environment cabinet.

The two time switches in the lower half of diagram work independently. The left switch controls the lights. The right time switch controls temperature by bypassing the high range thermostat during the low temperature period. When the cabinet is set for high temperature, contacts on the low range thermostat are closed, and the low temperature time switch is open, so that temperature is controlled by the high range thermostat. During the low range period, the time switch terminals are closed, thus bypassing the high range thermostat. The low range thermostat is thus in control.

The safety thermostat contacts at upper left are normally closed at all times. In the event of refrigeration failure, high temperatures within the cabinet shut off the lights.

The combination of outdoor temperature and the heat provided by the lamps made a heater unnecessary. It was therefore only necessary to provide for cooling. In considering the principle of the two temperature range system, it must be kept in mind that cooling in a refrigerator is dependent upon the time the compressor is in operation. The important difference between the high and the low temperature control, therefore, is the temperature at which the compressor is switched *off,* as well as when it is switched *on.* Two temperature controls, one for the high range and the other for the low, were connected in series to the refrigeration compressor. The control system was so arranged that the low range thermostat was in circuit at all times and the high range thermostat was cut into or out of the circuit by means of the time clock. Thus, during the high temperature period, the circuit of the low range thermostat was closed at all times and the operation of the compressor was controlled by the circuit being opened or closed by the high range thermostat. During the low range period, the time clock shorted out the high range thermostat, leaving the low range thermostat in control.

The high temperature control was a commercial thermostat designed for room air-conditioning systems. The low temperature device was a standard refrigerator control. For reasons discussed below under the section on "Humidity" it was necesary to change the original control from a pressure sensitive unit to one sensitive to temperature.

Both the high and low range thermostats were adjustable to operate over a wide temperature band. The latitude within which each operated at a given setting was also adjustable. In the present installation, the minimum temperature which could be maintained with the lights on was 8.3°C. It was thus possible to operate the cabinet at many different temperature settings—the low and high range being independent. At the same time the controls operated within a tolerance band of about plus or minus 1°C. at each setting. Went (1957) has given a good description of temperature control systems. In case it was desired to leave the unit at either a high or low temperature range, this could be accomplished by disconnecting the time switch. A thermograph tracing is shown in Figure 3 as an example of the operation of the cabinet. The temperatures were ones used in an actual experiment and are not meant to illustrate the extremes of temperature which can be achieved.

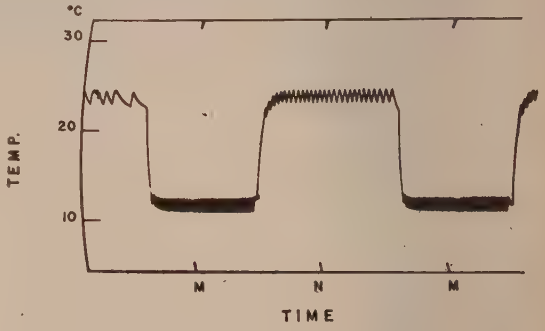

FIG. 3. Thermograph showing fluctuations of temperature in controlled environment cabinet. The large changes are brought about by a dual temperature control system operating on a diurnal basis and controlled by a time switch. "M" refers to 12:00 midnight and "N" to 12:00 noon.

A safety device consisting of an incubator switch was installed to prevent overheating of the cabinet in case of failure of the refrigeration system. This switch was designed to open at a pre-determined temperature to shut off the lights.

Temperature controls and light controls were completely independent.

HUMIDITY CONTROL

Relative humidity in Honolulu is usually more than 50%. The solution to the problem presented here may therefore be different from that required in a dry climate. As originally received, the refrigerator produced, at the temperatures desired, conditions of a constant 100% relative humidity within the box. The cause of this high humidity was failure of the coils to frost up at the relatively high temperature setting of the cabinet. The original expansion valve was therefore removed and a so-called "automatic" valve was used in its stead. This change in turn necessitated for the low temperature range, substitution of a thermostat in place of the original pressure sensitive control. The changes so made then permitted icing of the refrigerator coils at the temperature within the box, thus removing moisture from the air. As soon as the compressor stopped, the ice would melt from the coils and the condensate run down to a pan outside.

The control of humidity was not precise but was constant in its pattern of change at each temperature setting. The average relative humidity was, therefore, different at the low temperature range than at the high setting, there being an inverse relationship between the temperature and mean relative humidity.

Three adjustments could be made to manipulate the relative humidity. These were: the setting of the automatic valve which controlled degrees of frost on the cooling coils; the temperature differential between cut-in and cut-out on the thermostat; and the regulation of air velocity past the evaporation coils.

The moisture load of the air within the box was kept to a minimum by the use of drip pans underneath each plant in the cabinet. These pans were drained through a copper pipe sealed at the bottom of each pan. The copper pipes were connected by rubber tubing to a manifold situated at the bottom of the cabinet which then drained directly into an outside container.

CIRCULATION OF AIR

Ample air circulation was provided in the original refrigerator cabinet by a fan in continuous operation. Adjustment of the amount of air moved by the fan was provided by a pair of sliding sheet metal covers at the fan inlet shown in the top center of the photograph (Fig. 1) just above the plants.

OPERATION

The cabinet has given satisfactory service since the first unit was originally put into use in June, 1958. *Trifolium repens* plants have been grown successfully from cuttings over the entire vegetative and reproductive phases even in an unpainted cabinet. The authors have investigated the possibility of still higher light intensities by the use of very high output lamps. Information from the manufacturer on the heat output from such an installation would indicate that the heat produced would be beyond the capacity of the refrigeration system supplied as standard with the refrigerator. It should be noted that many plants are capable of adequate growth at the light intensity provided (Went 1957).

Provision for precise control of carbon dioxide would undoubtedly improve the performance of the cabinet. Efforts in this direction have been reported by Hiesey, Milner and Nobs (1959) and French, Hiesey, and Milner (1959).

Parts list used in installation.

1. 1 refrigerator—75 cu. ft., 5-door, reach-in type, with adjustable shelves and circulating fan.
2. 8 instant start fluorescent tubes with sockets—cool white. (F72T8/CW)
3. 4 ballasts for next size larger tubes. (89G490)
4. 4 incandescent lamps with sockets.
5. 2 24-hr. cycle time switches.
6. 1 automatic valve for refrigerator (to replace constant super heat valve). (No. 672 Detroit automatic expansion valve)
7. 1 thermostat—range 32° to 50° F. (Renco Tempera-Control No. 1410)
8. 1 thermostat—range 50° to 80° F. No. 241-6 White Rogers Temperature Control.
9. 1 safety thermostat—range 70-110° F. Incubator heater thermostat.
10. 1 air volume control valve for fan—sheet metal shop construction.
11. 10-20 plant container drip pans connected to manifold which in turn is directly connected to outside of box—sheet metal shop construction.
12. 1 pressure gauge for installation on compressor.

ACKNOWLEDGMENTS

The authors acknowledge support of Western Regional Committee W-58.

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BOG BRYOPHYTE ECOLOGY OF A SEDGE MAT

Introduction

This work was done from the middle of June to the middle of July 1959 at the University of Minnesota Forestry and Biological Station, The bog is at the southern extremity of the west arm of Lake Itasca in Itasca State Park, Minn., in the south half of the southwest quarter of section 15, T. 144 N., R.36 W. The purpose of the study was to identify the bryophytes on the mat, and to correlate their occurrence, extent, and the height of their apices above the water table with factors of pH, shading, and presence of other plants.

The author gratefully acknowledges the help of Mr. Willis Olson, biology teacher at the Minnesota Academy, Minneapolis, Minn., in identifying the mosses, and of Dr. M. F. Buell of the Botany Department, Rutgers University, New Brunswick, N. J., for his kind advice in the writing of this note.

General Description

The bog has definite sedge mat, tamarack, and black spruce zones (the respective dominants being Cyperaceae, *Larix laricina,* and *Picea mariana*). The sedge mat consists of a thick tough mat of roots and rhizomes, mostly graminoids ⅓ m in depth. Its top surface lies generally at water level; green parts of plants extend above water level. Depressions below the water table of the mat contain water, have no live graminoids, and are dispersed abundantly upon the mat. Some are holes in the mat extending through to the water below. This water is about ⅓ m deep and overlies loose organic debris about one m in thickness. The water is continuous with that of Lake Itasca.

Methods

A continuous 20 m line transect was made from the edge of the mat at the edge of the open lake water, across in a south-westerly direction, toward the first trees in the tamarack zone. The linear extent of bryophyte aggragations was recorded along the line. The maximum height of the apices of the bryophytes above the water table, pH of the water in the depressions, and the pH of the water on the surface of the bryophytes were recorded; the pH was taken with hydrion papers. The total extent of each bryophyte taxon in each bryophyte aggregate was deduced from the relative amount of stems of each in the samples taken into the laboratory for identification (Grout 1903-1908, 1938-1939, Jennings 1951).

The occurrence of vascular plants and their shading was determined by the linear extent, i.e., cover, of these plants along the line (Fernald 1950, Gleason 1952). The presence of live graminoids was noted along with the presence of upright dead graminoid stems and leaves; the latter were probably from the previous summer. To measure more adequately general shading intensity, the amount of overlap was determined; this was based on the cover occurring on more than one vertical level along the same places along the line.

Results and Conclusions

The only bryophytes on the sedge mat were mosses; none of these were of the Sphagnaceae. At the edge of the mat was *Drepanocladus aduncus* Kneiffii (Bland.) Warnst. It and *Leptodictyum riparium* (L. Hedw.) Warnst. were found generally over the entire mat; the former was more common than the latter. Near the tamarack zone were *Drepanolcadus aduncus polycarpus* (Hedw.) Warnst., *D. vernicosus* (Lindb.) Warnst., *Brachythecium oxycladon* (Brid.) Jeager and Sanerb., *Bryum psuedotriquetrum* (Hedw.) Schwaegr., and *Mnium affine* Bland.

Cover of forb-seedlings, extent of occurrence of graminoids, and amount of overlap increases from the edge of the mat to the tamarack zone. Over the entire mat, there was more overlap over moss aggregates than over places where there were no mosses. Over the first 2/3 of the mat, there was a greater extent of no cover over mossless segments than over segments where moss aggregates occurred. The extent of open areas over mossless segments decreased towards the tamarack zone, whereas the open areas over moss segments stayed the same over the entire mat.

In general, increase in density of the forb cover and shading due to tamarack trees was associated with increased height of mosses and increased number of taxons. These environmental factors and moss phenomena increased in appearance and intensity toward the tamarack zone. Toward the tamarack zone, the extent of mosses increased. Near the tamarack zone, some moss aggregates formed low flat hummocks; the mosses here were less dependent upon graminoid stems for support and attachment. These were often growing upon moss peat, which first occurred here in the sedge mat. The peat was mostly *Drepanocladus aduncus.* The mosses on the sedge mat were never floating; they were always attached to the floor of the sedge mat or to upright parts of graminoids, or growing on moss peat.

A comparison of amounts or intensity of environmental factors with certain moss phenomena, without regard to position upon the mat, gives the following: overlap and presence of graminoids increases with increasing extent by mosses; increasing overlap and forb-seedling cover is associated with increasing height of moss apices above the water table; and increase in forb-seedling cover is associated with increasing numbers of moss taxons.

The pH of the water on the moss stems and leaves was 5.6-6.0 over the entire mat. The pH of mosses was consistently lower than that of the lake, (6.6), and that of the water in the depressions (6.0-6.8).

The forb-seedlings in order of decreasing cover include: *Menyanthes trifoilata, Calla palustris, Betula pumila,* and *Salix pedicullaris.* Others on the transect are *Sagittaria, Potentilla palustris, Caltha palustris, Impatiens Lysimachia terrestris,* and *Galium.*

The graminoids are mostly *Calamogrostis canadensis, Eleocharis robbinsii, Carex prairea, C. aquatillis,* and some non-sexually reproducing unidentified ones. *Calamogrostis canadensis* occurred densely and exclusively along the edge of the mat.

Widely scattered *Eriophorum* and *Rumex britannia* occurred on the mat, but not in the transect. *Lemna minor* appeared on the water next to the mat and in the depression water in the first half of the mat. *Utricularia intermedia* appeared in the depression water on most of the mat. The only shrub on the transect near the tamarack zone was *Betula pumila.*

The interpretation of results is uncertain. Possibly factors other than those measured may have influenced the moss responses observed. Factors measured on the mat may have been at intensities within the ranges of requirements and tolerances of the mosses, thus resulting in responses not measured or below measurability relative to the methods used.

Method of measure of graminoid cover needs to be improved. Shadow extension by taller plants due to the angle of the sun with the zenith was noted but not measured. Seasonal changes were not noted. Additional samples and measurements may have to be taken in order to determine the significance of the results.

SUMMARY

From the edge of the mat at the edge of Lake Itasca, to the tamarack zone, cover increased in the herb layer, and near the tamarack zone was supplemented by tamarack tree shade.

With this increasing shading were associated: increasing numbers of moss taxons, increased height of mosses over the water table, and increased thickness and spread of mosses.

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SOME MEASURES OF UNIFORMITY IN VEGETATION ANALYSIS

In the study of natural vegetation it is necessary to divide the vegetation into types which are described separately and compared. This is true whether one prefers to treat vegetation as a classifiable subject which can be divided objectively into separate units as held by the Zürich-Montpellier and Scandinavian as well as other schools of phytosociology or whether one prefers to treat all vegetational variation as continuous where all division lines are arbitrary and may be drawn where suitable for the purpose at hand as held in the recent study of the vegetation of Wisconsin by Curtis (1959). The types may be narrowly defined as is the case with most of the elementary types described by Scandinavian authors, or the types may be very broadly defined including a considerable range of vegetational variation as done by Curtis. The results obtained by such different methods cannot be readily compared. It is therefore of considerable interest to obtain a measure of the narrowness of definition of the types. This amounts to measuring the uniformity, or homogeneity, of the plots selected for analysis and the uniformity, or homotoneity, of vegetation type; the term homoteneity was introduced into plant sociology by Nordhagen (1943, see also Dahl 1957 p. 46). In the case of homogeneity different plots of the same size taken from an individual stand are compared, in the case of homotoneity, comparable plots from different stands of the same type are compared. Following the terminology of Braun Blanquet (1951) the percentage presence of a species in a set of samples of equal size from one stand is termed the frequency of the species, while the percentage presence of a species in a set of equivalent or equal sized samples of different stands is termed the constancy of the species.

If two samples of a vegetation are taken, these can be compared by a suitable index of floristic similarity. Such indices are usually based on species presence, but may be extended to include other characters as well, such as species cover. If the number of species in the first sample is a, in the second b, and the number of species shared by the samples is c, one measure is

$$K_s = \frac{2c}{a+b} \quad \text{(Sørensen 1948)}$$

This index of floristic similarity is actually a variant of the index proposed by Jaccard (1902).

$$K_j = \frac{c}{a+b-c}$$

since

$$K_s = \frac{2K_j}{1+K_j}$$

Thus a value of K_s corresponds to a value of K_j whatever the values of a, b and c.

If a set of samples is available, the indices of floristic similarity of pairs of samples may be averaged for all pairs and in this way a measure of uniformity for the whole set may be obtained. This index is 1 if all samples contain the same species and 0 if all samples have entirely different sets of species.

The Sørensen index of floristic similarity may also be written, restricting ourselves to indices based on species presence

$$K_s = 2 - \frac{a+b-c}{\frac{1}{2}(a+b)}$$

$a+b-c$ is the number of species of the two samples taken together (S_2), and $\frac{1}{2}(a+b)$ is the mean number of species in the two samples (S_1). Thus

$$K_s = 2 - \frac{S_2}{S_1}$$

An index of uniformity based on comparison of pairs of samples by means of the Sørensen or Jaccard indices of floristic similarity is thus an expression of the way in which the total number of species in a set of samples increases with increasing number of samples. If the increase in species-number as a function of number of samples is known, the indices can be predicted (Dahl 1957 p. 57 f.).

Another criterion of uniformity widely used by Scandinavian phytosociologists is based on the shape of the constancy or frequency curves. All species with percentage presence higher than 80% are placed in frequency or constancy class V, those with percentage presence between 80 and 60 in class IV, those with percentage presence between 40 and 60 in class III, those with percentage presence between 20 and 40 in class II and those with percentage presence up to 20% in class I. The number of species is presented in a diagram or a curve.

It has been found (Palmgren 1917, Raunkiaer 1918, Du Rietz, Fries, Osvald und Tengwall 1918) that if sufficiently large samples from a homogenous vegetation or a set of samples of a uniform vegetation type are combined to construct a frequency or constancy curve, this curve exhibits certain regularities. The number of species in class V is higher than in class IV. If an alien element is introduced in the material this relation is reversed. Thus the relation between number of species in class V and IV can be used as a criterion of uniformity.

It was shown by Williams (1950, see also Dahl 1957 p. 41 f) that the shape of the constancy and the frequency curves depend on the way in which the total number of species sampled increases with increasing number of samples. If the total number of species sampled as a function of number of samples is known, the number of species in each of the constancy classes can be calculated. Thus the ratio class V/class IV criterion of uniformity is again an expression of the increase in species number with increasing number of samples.

Curtis (1959 p. 79 f.) has introduced a new measure of uniformity which is termed the index of homogeneity. First the mean number of species in a set of samples and the percentage presence or in the terminology employed here constancy percentages for all species are calculated. Then the species with the highest constancy percentages are selected, and as many as corresponds to the mean number of species per sample. These species are termed the prevalent species. The ratio between the mean number of prevalent species per analysis and the mean number of species per analysis is calculated; this is the index of homogeneity. The most convenient method of calculation of this index is by adding the constancy percentages of the prevalent species and the constancy percentages of all species and dividing the two figures obtained.

It is obvious that the index of homogeneity depends on the shape of the constancy curves; if the constancy curve for a set of samples is known the index of homogeneity can be calculated. Thus Curtis' index of homogeneity is another expression of the way in which the total number of species sampled increases with increasing number of samples.

The increase in species number with increas in area sampled or number of plots sampled is thus of fundamental importance in the evaluation of all the indices discussed. Fisher (In Fisher, Corbet and Williams 1943) has developed an extremely useful mathematical model originally for animal communities which later also has been used for plant communities. It does not apply to very small and very large samples (for references and discussion see Dahl 1957), but for sample sizes normally used in phytosociological work predictions based on the Fisher mathematical model give results which remarkably accurately tally the actual observations for the most diverse communities. In the Fisher model the species number is given by the relation

$$S = \alpha \log (1 + qx)$$

where x is area or number of equivalent samples and α is a measure of an intrinsic property of the population sampled termed the index of diversity. The q is a constant. Napierian logarithms are used throughout. The curve is defined if the mean number of species per sample (S_1) and the index of diversity is known. If qx is so large that the term 1 can be neglected a linear relation between log area or number of samples and species number is obtained. The slope of the curve gives the index of diversity. If q is large, i.e., the ratio S_1/α is large and the total number of species in n samples is S_n, then

$$\alpha = \frac{S_n - S_1}{\log n}$$

This is a convenient method for calculation of the index of diversity, but the limitations of the method should be kept in mind.

For a more exact determination of the ratio S_1/α, a quantity which may be termed the index of uniformity, the chart Figure 1 has been prepared. Number of samples (n) is given along the horizontal axis and the ratio S_n/S_1 along the vertical axis both on log scales. The lines give the corresponding values of the index of uniformity. S_1 is directly calculated from the observations and when S_1/α is known the correct value of α is obtained.

In the Fisher model the Sørensen index of floristic similarity is a function of S_1/α, high values of S_1/α corresponding to high indices of floristic similiarity. The curve giving the relation between expected value of K_s and the index of uniformity is given by Dahl (l.c.p. 58).

The constancy or frequency curves are functions of S_1 and α, and the ratio between species number in class V and IV is a function of the index of uniformity alone. If the index of uniformity is higher than 1.2 the number of species in class V is expected to be larger than class IV, the ratio increasing with increasing values of the index of uniformity. Curves aiding the calculation of number of species in the different constancy or frequency classes are given by Dahl (l.c. p. 42-43) for sets of 5 and 10 samples.

The theoretical curve for Curtis' index of homogeneity as a function of the index of uniformity is given in Figure 2. The curve applies to a large number of samples. If the number of samples is small and especially if the index of uniformity is low, the expected values of Curtis' index of homogeneity are somewhat higher. The minimum value of a set of 10 samples is 10% if no species is shared by the samples, while the corresponding value in a large number of samples is close to zero. Curtis (l.c. p. 80) noted a linear relation between his index of homogeneity and the logarithm of the index of uniformity. The curve in Figure 2 is not exactly a logarithmic function, it is a complicated integral function, but has a general shape quite similar to a logarithmic function.

In Figure 2 observed values of Curtis' index of homogeneity have been compared with the corresponding values of the index of uniformity. The chart Figure 1 has been used in calculating the indices of uniformity since in many cases the simplified method may introduce appreciable errors. Triangles refer to data from my study of Rondane for vegetation types where 10 or more samples are available. Dots refer to values from Wisconsin communities given by Curtis (l.c. table IV-2 p. 517). It will be seen that the observations are reasonably well grouped around the theoretical curve. Thus Curtis' index of homogeneity can be predicted from the index of uniformity.

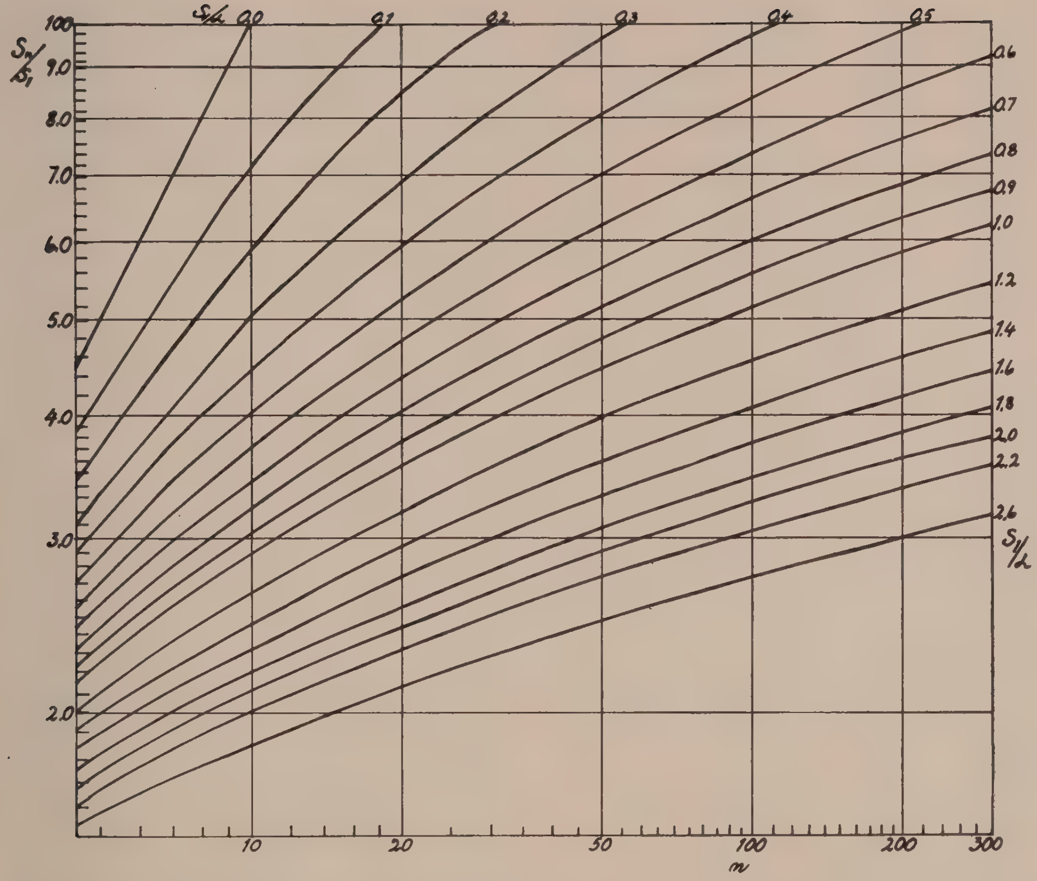

FIG. 1. Chart for the determination of the index of uniformity (S_1/α) from the number of samples (n) and the ratio between the total number of species sampled (S_n) and the mean number of species per sample (S_1). Both n and S_n/S_1 are given in logarithmic scales.

A control of uniformity can also be based upon the variance of S_1. In the Fisher model the expected variance is given as a function of the index of uniformity and the index of diversity; a graph of the relationship is given by Dahl (l.c. p. 55). The observed variance can be compared with the expected variance and the discrepancy tested by standard statistical procedures. If some of the samples are heterogenous, indicating that some alien floristic element has crept in, the number of species in the sample is increased in relation to the other samples and this will increase the variance. This is a sensitive test of uniformity but not an infallible one. By selecting samples from different vegetation types which happen to have the same number of species per sample a clearly heterogeneous table may be made but with zero variance of S_1.

It will be seen from Figure 2 that the observations from the Wisconsin communities are grouped in the lower left corner and the Rondane communities in the upper right corner of the graph. This is due to differences in the techniques employed. The vegetation types of Rondane are very narrowly defined corresponding to rather uniform associations, while vegetation types of Curtis are very broadly defined, including many associations in the sense of European phytosociologists (Curtis l.c. p. 478). If the entire material from Wisconsin is taken to be representative of the Wisconsin vegetation as a whole, the index of uniformity of the Wisconsin vegetation can be calculated. There are altogether 1167 samples with a mean number of species per analysis of 39 (calculated from Curtis table IV-2 p. 517) with a total of 867 species (Curtis l.c. p. 487). This gives an index of uniformity of 0.31. Some of the vegetation types described by Curtis have indices of uniformity lower than this—thus beach (0.18), exposed cliff (0.20), shaded cliff (0.24) and lake dune (0.29) communities. Chances are that any two samples taken from one of these communities will be as different as any two samples taken at random from the entire Wisconsin vegetation.

For comparison 445 analyses of samples from Rondane have been published (Dahl 1957) with a mean number of species per sample of 19.0 and altogether 429 different species giving an index of uniformity of 0.21 for the entire vegetation of Rondane. In the comparison of these figures with corresponding figures for the vegetation of Wisconsin the differences in methods should be kept in mind.

Curtis (l.c. p. 478) compared his Wisconsin communities with my communities from Rondane, a mountain

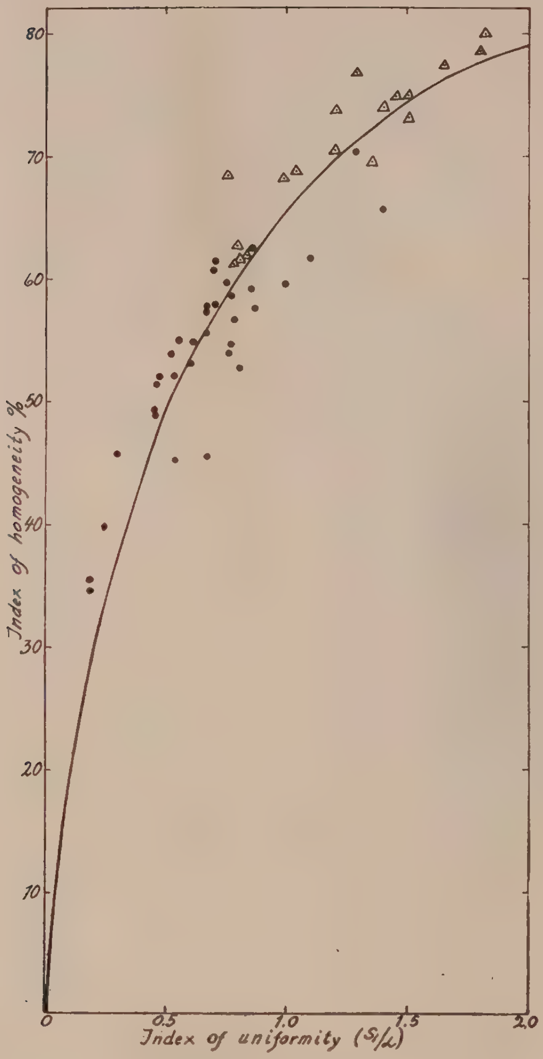

FIG. 2. The relation between the index of uniformity (S_1/α) and the index of homogeneity (Curtis 1959). The curve represents the theoretical relation based on the Fisher model of plant communities, triangles represent observations from vegetation types in Rondane, South Norway and dots observations from vegetation types of Wisconsin. Further explanation in text.

area in South Norway, as to number of species per analysis and the indices of diversity. From the comparison he concluded that the vegetation in Wisconsin exhibited a greater floristic richness than the vegetation of Rondane.

This may be true, but cannot be concluded from a mere comparison of indices of diversity and number of species per analysis apart from the level of uniformity on which the work is performed. Curtis worked with rather large samples and only the tree layer was tested for homogeneity (l.c. p. 71). Since the groundlayer vegetation may vary quite appreciably under a homogeneous tree layer a quite diverse groundlayer vegetation might be included in the samples. This will tend to increase the value of S_1. Secondly the uniformity of his vegetaion types is low i.e. the ratio S_1/α is low and consequently the value of α is high. Thus the differences in S_1 and α may only be a reflection of differences in methods and not a reflection of any intrinsic property of the vegetation studied.

SUMMARY

It is pointed out that most measures of uniformity or homogeneity in vegetation analysis can be predicted if the mean number of species per unit area or sample and the index of diversity, a parameter expressing the increase in total number of species sampled as a function of area or number of samples, are known. A new index of uniformity is proposed, defined as the ratio between the mean number of species per sample and the index of diversity. The relationships between the index of uniformity and other measures of floristic similarity or homogeneity are discussed and the results applied to some of the data recently published by Curtis (1959).

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THE USE OF THE OPTICAL SQUARE FOR SAMPLE PLOT LAYOUT

Introduction

Over the years there have been numerous investigations into the many aspects of forest sampling—efficiencies of plot size and shape, methods of plot layout, adequacy of the sample, etc. The published papers are too numerous to list here, although the recent paper by Lindsey, Barton and Miles (1958) is worthy of mention.

In North America, when a square or rectangular plot is to be used in field sampling it is usually laid out by one of the following methods:

a) Method I. Widely used for square plots:—a good staff compass set up at the center of the plot, positions diagonals of the square. Plot boundaries should then be run from the established corners to adjust any errors.

b) Method II. A staff compass is set at a plot corner and a 90° angle turned off and boundary measurement establishes the next corner. Since this method usually involves three compass set-ups, it is not generally used for square plots, but does find some application to rectangular plots of 1/5 or ½ acre, for example.

c) Method III. A right angle may be established by using the time honored triangle formula: base 3—height 4—hypotenuse 5. This method lends itself to inaccuracies and trees may become a nuisance by obstructing measurements of the sides of the triangle.

In Australia, Great Britain and Europe, the use of an optical square for rectangular plot layout has found favor when accuracy and efficiency is desired. Following is a description of the instrument and its use.

The Instrument

The instrument, a reflecting prism generally called an optical square or sometimes a pentagonal prism, is simply a glass prism designed to take advantage of Snell's law of refraction and the critical angle of glass.

Mounted in a metal holder, this small prism meets most requirements of an ideal field instrument—light weight, vest pocket size, will withstand hard use, permanently calibrated, adjustments never needed, simple to operate, no scales to read, accurate and versatile.

Method

The following procedure is for the layout of 0.1 acre square plot using a two man crew, instrument man and chain man, hereafter called "A" and "B" for convenience.

1. "A" sets up the 5.5 ft staff bearing the instrument at a point which will bisect a boundary line, and sets a 4 ft reference stake some 20 or 30 ft away. This line of sight or reference line—instrument to reference stake—will become the center line of the plot and may be aligned on a definite bearing if desirable; for our purpose assume it to be north.
2. "B" proceeds west with a steel tape from the instrument and at a right angle to the reference line for approximately 33 ft. "A" holding the tape uses the prism to align a corner stake held by "B" into the exact location of the S.W. corner—33 ft from the instrument and at a right angle to the reference line (Fig. 1).

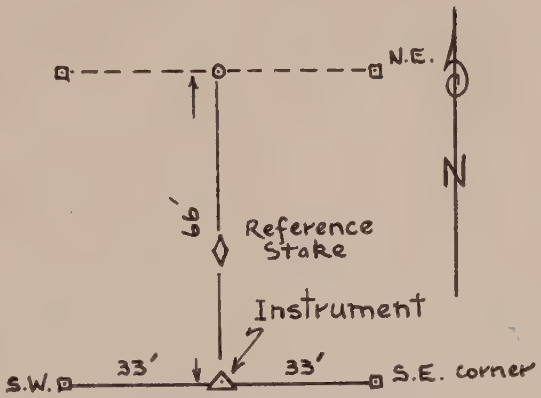

Fig. 1. Method of laying out a one-tenth acre square plot by the optical square.

3. "A" proceeds to the S.E. corner with the tape and at 66 ft, positions this corner by aligning the instrument staff and the S.W. corner stake, where "B" has remained to hold the tape.
4. With the tape, "B" measures off 66 ft north from the instrument point past the reference stake to the opposite boundary and sets a center point boundary stake in line with the reference stake and instrument. This becomes the mid point of Boundary Line 2, Fig. 1.
5. "A" replaces the instrument staff with a stake and proceeds to the opposite boundary (#2). Here he sets up the instrument at the boundary mid point and sights back on the reference stake.
6. Procedure as in (2) and (3) above is repeated to establish the remaining two plot corners.

Discussion

This prism method for angular plot layout is superior in both layout time and accuracy to the other methods mentioned. Levelling of the prism, which is necessary for proper use, is accomplished by aligning any handy upright image, such as a tree, a stake, or any improvised plumb line, perpendicular in the prism.

When results approaching transit accuracy are desired, a tripod should be substituted for the staff and a plumb bob used to position the instrument and the corner stake. On a slope, the reference stake will need to be set within the line of horizontal sight. Hence, sighting up slope is more practical than sighting down slope. For example, with a 100% slope, and an instrument height of 5 ft, the reference stake should not be over 5 ft away.

Experience has shown the method to be ideally suited to a two-man crew, in fact a three-man crew cannot to any practical measure improve on the two-man crew layout time. In most of the sampling and plot designs, in which the author is experienced, a two-man crew has been found the most efficient unit when the work is measured by man days.

In many types of sampling, work methods designed for a three-man crew can usually be changed to suit a two-man crew without loss of efficiency. The key to successful modification is usually an instrument. Such is the case of the optical square which effectively replaces and improves on the compass in plot layout work.

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A FURTHER APPLICATION OF LENGTH-WIDTH VALUES TO THE DETERMINATION OF LEAF-SIZE CLASSES

A major obstacle to more extensive use of leaf-size classes in vegetational analysis, as originally proposed by Raunkiaer (1916), is the difficulty and tedium involved in actual measurements of leaf area. Many methods of measurement (weight-area relations, graph paper, planimeter) have been proposed but none has proved satisfactory enough to be used extensively. Recently Cain *et al.* (1956) and Cain and Castro (1959) found that for tropical rain forest species leaf area values could be determined with reasonable accuracy by the formula, 2/3 length x width. Because of the potential usefulness of this technique, further tests in other vegetation types seem desirable, particularly in temperate regions where there are significant numbers of lobed and dissected leaves which are almost absent from rain forest.

An opportunity to make such a test arose during a life-form and microclimate study (Cooper 1958). This note summarizes results of application of the 2/3 LW rule and supplies additional observations on uses of length-width values in determination of leaf-size class.

Location of Area and Methods

This study was carried out on the E. S. George Reserve in southeastern Mich. from March to November, 1957. The Reserve is in south-central Livingston County approximately 23 miles northwest of Ann Arbor, Mich. The study was carried out within the Big Woods, the largest tract of second-growth oak-hickory woodland on the Reserve.

Details of methods of sampling microclimates and vegetation and the results of these studies have been reported by Cooper (1958). Leaf-size data were obtained from voucher specimens of all species encountered in sample plots. Representative leaves were chosen from the specimens and their areas determined by tracings on millimeter graph paper and by the 2/3 LW rule.

Results

A comparison of leaf-size class distributions in the entire Big Woods flora of 228 species (Table I) showed that little error was introduced by assigning size classes on the basis of the 2/3 LW rule. Only 12 species were misclassified. As the errors were spread among all leaf-size classes that in any single class was negligible.

When errors did occur, they were generally in the direction of an increase in leaf area, rather than a decrease. Of the 12 species incorrectly placed, 9 were to higher classes and only 3 to lower; 66% of all leaves had larger areas by the 2/3 LW rule and only 34% had smaller areas. Generally, elliptic, ovate, oblanceolate, obovate, or spatulate leaves were over-estimated. Orbicular leaves, on the other hand, were consistently under-estimated. The errors were never large and generally fell within ± 10%.

Table I. Raunkiaerian leaf-size classes in Big Woods based on actual area and ⅔ LW determinations

Class	Actual Area		2/3 LW	
	Number	Percentage	Number	Percentage
Aphyll (leafless)	3	1.3	3	1.3
Leptophyll (<25 mm^2)	6	2.6	6	2.6
Nanophyll (<225 mm^2)	45	19.7	42	18.4
Microphyll (<2025 mm^2)	132	58.0	133	58.4
Mesophyll (<18225 mm^2)	42	18.4	44	19.3
Macrophyll (<164025 mm^2)	0	0.0	0	0.0
Megaphyll (>164025 mm^2)	0	0.0	0	0.0
Total	228	100.0	228	100.0

The largest and most frequent errors were found in classification of lobed leaves. Of these, 18% (4 of 22) were misclassified (always to the next larger class) whereas only 4% (8 of 203) of non-lobed leaves were misclassified. The size of the positive errors for lobed leaves suggested that some factor other than 2/3 should be used (Table II). For either palmately-lobed leaves, or obovate leaves and leaflets with deeply-toothed upper margins, or pinnately-lobed leaves with narrow or shallow sinuses, a factor of ½ gave adequate results. Average area was estimated to within 1% for palmate leaves (e.g. *Acer, Ribes*) and for shallowly pinnately-lobed leaves (e.g. *Quercus velutina* and *Q. rubra* shade leaves). The error for the obovate leaflets (e.g. *Agrimonia, Sanicula*) was within 5% of actual average area. For pinnately-lobed leaves with deep sinuses (e.g. *Quercus velutina* sun leaves, *Gerardia flava*) a factor of ⅓ gave an estimate of area within 2% of average actual area. Six of 7 of these species were estimated to within ± 10%.

Leaf length, width, and area data for plants in the arid portions of south Australia (Cannon 1921) offered an opportunity for a test in another vegetation type. Here the results (Table III) were even more striking than in the example of temperate vegetation. Using the 2/3 LW rule only one of 46 leaves was misclassified and resulting distributions of leaves in size classes were virtually identical.

Discussion

In samples of temperate and of arid vegetation, use of the 2/3 LW rule gave sufficiently accurate estimates of leaf area for assignment of leaves to the correct Raunkiaerian size class. Thus, the data show that the rule is applicable to vegetation other than tropical. As

TABLE II. Comparison of average actual area of lobed and palmate leaves in Big Woods flora with averages of other measures of area determination

Leaf or leaflet character	No. spp.	Average actual area (cm²)	Average area ⅔ LW (cm²)	% error	Average area ½ LW (cm²)	% error	Average area ⅓ LW (cm²)	% error
Palmately-lobed	5	4142	5517	33%	4138	– 1%	2758	–34%
Obovate, upper margin deeply toothed	6	476	597	26%	452	– 5%	300	–37%
Pinnately-lobed, shallow and/or narrow sinuses	10	1663	2208	33%	1657	– 0.5%	1104	–34%
Pinnately-lobed, deep and/or wide sinuses	7	2100	4125	97%	3100	48%	2062	– 1.5%

Cain and Castro (1959) point out, this technique makes estimation of leaf area and assignment to size class relatively simple, thus eliminating a basic problem in the use of leaf-size data in vegetational analysis.

Areas of lobed leaves obtained by the 2/3 LW rule were less accurate than areas of non-lobed leaves and other constants were tried. The use of the constant values ½ and ⅓ gave relativelv accurate measures of area for frequently-encountered patterns of leaf lobing without greatly decreasing ease of application. The choice of factor for a given leaf occasionally was difficult, the factor varying for the same plant in different areas or under different conditions. The overall increase in accuracy, however, seemed to justify the use of these lower constants for lobed leaves.

TABLE III. Raunkiaerian leaf-size classes in the vegetation of arid portions of south Australia (adapted from Cannon 1921) as determined by actual area and ⅔ LW rule

Class	ACTUAL AREA		2/3 LW	
	Number	Percentage	Number	Percentage
Aphyll	0	0.0	0	0.0
Leptophyll	5	10.8	6	13.0
Nanophyll	21	45.7	20	43.5
Microphyll	20	43.5	20	43.5
Mesophyll	0	0.0	0	0.0
Macrophyll	0	0.0	0	0.0
Megaphyll	0	0.0	0	0.0
Total	46	100.0	46	100.0

It is concluded that the 2/3 LW rule can be used to assign most species in temperate vegetation to Raunkiaerian leaf-size classes. For lobed leaves, factors of ½ and ⅓ are recommended, the appropriate factor being determined by the size of sinuses.

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THE COMPARATIVE STUDY OF BEHAVIOR[1]

This book represents an attempt by a number of contributors to present empirical and theoretical material of current concern to comparative psychologists. The topics discussed include innate behavior, sensory processes, and the genetic bases of individual differences as well as motivation, learning, and comparative social psychology. The preface states that each contributor was permitted to develop his chapter as he saw fit and that little revision by the editors was deemed necessary when the finished product was submitted. The decision to adopt a policy of editorial *laissez-faire* was, in this reviewer's opinion, most unfortunate, since the contributors differed markedly with respect to the manner in which they treated their material. Some wrote for the graduate student and for the specialist, providing detailed reviews and critical evaluations of the experimental literature with which they were concerned. Others apparently wrote for the beginning undergraduate and for the interested layman, choosing to ignore the more difficult empirical and theoretical aspects of their topics. The net result is a book that will satisfy neither the expert nor the neophyte, for the former will find much that is superficial and trivial and the latter much that is complex and detailed.

A book of such uneven caliber is difficult to evaluate. It appears that the most satisfactory form of review would be to discuss several chapters which are antipodal in quality: that is, those which are outstandingly poor by virtue of their superficial character and, in some cases, their egregious errors or are outstandingly good by reason of their detailed analyses and their comprehensive coverage of the literature. In the former category we can include the chapters by Waters, Caldwell, and Rethlingshafer and in the latter category the chapters by King and Nichols, and Riopelle.

Consider Caldwell's contribution entitled: "Theoretical Foundations of Comparative Psychology." It begins with a brief historical introduction and then turns abruptly to discuss what Caldwell apparently considers to be the foundations of comparative psychology; viz, learning theory, theories of perception, "neoinstinctual theory," "Old's theory of brain stimulation," and Lewin's field theory. Since each "theory" is treated separately without providing a convincing rationale for its inclusion and since there is little attempt to relate one theory to any other theory, the reader is confronted with a virtual potpourri. Whether expert or neophyte, he will undoubtedly be at a loss to explain why, as a group, these theories constitute the foundations of psychology *qua* comparative, or for that matter why they constitute the foundations of any other area of psychology.

Under the category of egregious errors, we might include the fact that Caldwell specifies the fundamental problem of comparative psychology as one of ". . . understanding. . . . the differences and similarities between man and infrahumans." This, of course, represents a gross misunderstanding of the comparative method. Indeed, the problem that Caldwell considers fundamental is not, as it is stated, a central problem at all, except perhaps for those who believe the Cartesian man-brute dichotomy still processes merit.

The chapter by R. H. Waters on the "Nature of Comparative Psychology" attempts to treat the subject matter, methodology, and aims of comparative psychology as a scientific discipline. Waters was apparently writing for the neophyte, for much of what he wrote is elementary. Now there is, to be sure, no reason to quarrel with a chapter simply because it is elementary, but there is every reason to quarrel when so much of that chapter is also superficial. As a case in point, consider the definitions that Waters offers of comparative psychology and comparative ethology. He tells us that the subject matter of comparative psychology is ". . . the behavior exhibited by an animal in adjusting to the internal and external pressures that impinge upon him" and that the subject matter of comparative ethology is ". . . . the life ways and habits of animals." Surely it is not unreasonable to insist that there is a difference between a definition that is elementary and one that is trivial. And surely it is also not unreasonable to insist that this difference is important even though one is writing for the beginning student. Waters then compounds the sin of having offered two trivial definitions by, in turn, offering a third definition that is grossly misleading. After nearly three pages of discussion, he concludes that behavior, as the psychologist defines it, has the ". . . properties of autonomy, persistence, variability, and docility." Does this mean that the many sterotyped responses exhibited by animals lie outside the province of the psychologist? Should not the psychologist be interested in studying the species-specific responses to which ethologists have called attention, responses which have aroused so much interest precisely because they are inflexible and are resistant to environmental influence? It is fortunate that many comparative psychologists are currently investigating response systems which do not exhibit the properties to which Waters points. It would be most unfortunate if the beginning student, after reading Water's chapter, were to conclude that these investigations are not "psychological" because they are not really concerned with "behavior."

Another disappointing chapter is the one entitled "Biological Approach to Motivation," by D. A. Rethlingshafer. Indeed, in this chapter there is so much that is superficial that the neophyte might well question whether there is any real empirical and theoretical substance to what Rethlingshafer calls "motivational psychology." But in addition to being superficial, the chapter has a rather obvious amateurish flavor which at times proves disconcerting and confusing. Thus, Rethlingshafer speaks of "instincts being released into behavior" and of "response selecting" as being inevitable provided "that there is some behavior." She also speaks of "two concepts—drive and drives." This reviewer can very well empathize with a reader attempting to distinguish between Rethlingshafer's use of drive-in-the-singular, drive-in-the-plural, and "need drive," which is the term she employs to designate the singular of drive-in-the-plural.

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[1] Waters, Rolland H., D. A. Rethlingshafer, and Willard E. Caldwell (editors) 1960. Principles of comparative psychology. (symposium) McGraw-Hill Book Co., Inc., New York, Toronto, London. ix + 453 pp., 85 figs., 14 tables. $7.95.

The chapters by Riopelle and by King and Nichols stand in marked contrast to those just reviewed. They are well written and well organized, and they treat the material they purport to treat in a manner that will satisfy the expert and will also serve to instruct the neophyte.

King and Nichols treat "problems of classification," dealing first with selected aspects of zoological taxonomy and then with the possibility of establishing a taxonomic system of comparable scope and precision for the comparative study of behavior. They are to be commended for their concise and thorough presentation of the foundations of zoological classification; indeed, it would be hard to find a more comprehensive and yet succinct introduction for the beginning student of either zoology or comparative psychology. With respect to their discussion of behavioral taxonomy, one might reasonably wish that King and Nichols had been more selective in choosing systems of potential classificatory value. Nonetheless, they treat the many problems facing the psychological taxonomist in a manner that the expert will likely find both informative and provocative.

The chapter by A. J. Riopelle provides a detailed examination of several experimental arrangements that have been used by psychologists to investigate complex cognitive events in animals and, in addition, offers a critical evaluation of the evidence that psychologists have adduced to explain these events. Such topics as learning, reasoning, imitation, and learning sets are treated in a manner that reveals the author's precise knowledge of the literature and his first-hand awareness of the methodological problems involved in studying cognitive processes. Riopelle's discussion of observational learning and imitation is particularly distinguished for it presents a sophisticated and well-balanced examination of a most controversial research topic. It is to be emphasized that Riopelle assiduously avoids the facile conclusions and the shallow generalizations which several contributors of this book apparently consider to be the proper diet for the beginning student. Although the beginner will undoubtedly find this chapter difficult, he should certainly be urged to persevere in his attempt to understand all that it offers.

It is a problem to write a brief peroration when one is reviewing a book that presents a striking admixture of the trivial and the profound. Perhaps it will be sufficient simply to state that for the past several years there has been a need for a comprehensive, up-to-date text in comparative psychology which, unfortunately, the publication of this book does not substantially reduce.

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COMPARATIVE ETHOLOGY OF BIRDS[1]

Two doctoral theses constitute the first numbers of a new ornithological series sponsored by the Nuttall Ornithological Club of Cambridge, Massachusetts. Both numbers deal with the same general subject—the analysis of factors and processes involved in pairing and mating that bring reproductive isolation in closely related sympatric species. The first study was done on the eastern and western meadowlarks (*Sturnella magna, S. neglecta*) by Wesley E. Lanyon at the University of Wisconsin; the second study is concerned primarily with four species of herons and egrets, *Butorides virescens, Ardea herodias, Dichromanassa rufescens, Leucophoyx thula,* and was made by Andrew J. Meyerriecks at Harvard University. Both studies are intensive and detailed analyses of high merit in the relatively new area of ethology.

The two groups of birds offer many interesting contrasts. The two sexes in all species are very much alike in morphology and coloration, especially in the meadowlarks. In the herons and egrets, the color of the males' plumage and especially the "soft parts" of bill, buccal cavity, lores, and legs become brighter and flashy in the male during the breeding season. The two species of meadowlarks are distinguishable with difficulty by coloration but differ markedly in songs and call-notes. The species of herons and egrets differ greatly in color, but their vocalizations are limited in variety.

The two meadowlarks have nearly identical territorial and sexual behavior and food habits. Territories of the two species are mutually exclusive. The western meadowlark, however, occupies dry upland habitats and the eastern meadowlark wetter areas with taller, denser grasses. This difference in habitat presumably evolved during the Pleistocene when the two populations were geographically isolated and while speciation was being completed. The herons and egrets occur in marshy habitats. Related species have nearly world-wide distribution.

Interbreeding between the two meadowlarks is prevented primarily by the females responding to the species difference in the call-notes of the males. Call-notes are inherited, but isolated young birds will learn to give the primary song of either species. Interbreeding in the herons and egrets is prevented by species differences in coloration and behavior. Sexual stimulation for pairing and mating in meadowlarks depends principally on vocalizations, in the herons and egrets on their highly ritualized displays and ceremonies.

Much space in the two papers is devoted to the detailed description and analysis of songs and call-notes on the one hand and of displays and behavior patterns on the other. This involved tape recording of calls and songs in meadowlarks, their spectrographic analysis, hand rearing of birds, as well as detailed field work. The study of the meadowlarks was concentrated on 100 acres of farmland near Madison, Wisconsin, where both species were nesting, and extended over three full seasons and part of a fourth.

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[1] Lanyon, Wesley E. 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. Publications of the Nuttall Ornithological Club, No. 1: i-viii, 1-67, 31 pl. Cambridge, Mass.

Meyerriecks, Andrew J. 1960. Comparative breeding behavior of four species of North American herons. Publications of the Nuttall Ornithological Club, No. 2: i-viii, 1-158, 15 pl. $2.00 paper, $3.00 cloth.

(Both numbers are obtainable from Massachusetts Audubon Society, Drumlin Farm, South Lincoln, Massachusetts).

Meyerriecks spent two full seasons and part of a third on a concentrated study of the green heron, *B. virescens,* on Long Island, New York, and several months on this and other species in Florida and Mexico. His data were obtained entirely by field observations with binoculars and telescope.

If these two numbers set the standard, we can expect very important contributions in future publications of this series. The present issues give us a much better understanding of the behavior and ecology of two very diverse groups of birds and serve as a challenge to obtain similar information on other species.

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All About a Mosquito[1]

There is a sort of law of increasing returns in biology, that the more that is known about a particular organism or phenomenon, the more can be learned. This makes *Aedes aegypti,* the yellow fever mosquito, an ideal subject for research, particularly since Sir Rickard Christophers has now pulled all the bits of information together in this immense book with its many hundreds of bibliographic references. One wonders whether any species of non-domesticated animal has been so well studied—classing *Drosophila* and the honey bee as "domesticated" and, rather doubtfully, *aegypti* as "wild." Yet, thumbing through the book, one is impressed by how much we have yet to learn, how many significant experiments and observations remain to be made. This is particularly true at the levels of ecology, behavior and evolution.

The details are all here in these 700 large, fact-filled pages. Sir Rickard starts with an historical sketch. He then has a chapter on systematics and distribution—and one is impressed by the fact that there is still no certainty about the "proper scientific name" for this extremely well studied species. Then there are chapters on bionomics, on relation to disease and control, on techniques for study. After this there are three chapters on the egg stage and embryology, six on the larva, two on the pupa, and fifteen on the adult. The animal doesn't have a hair that hasn't been peered at and described by many authors, doesn't make a wriggle that hasn't been analyzed and charted from stimulus to response. Yet very large questions remain to be answered.

Aedes aegypti is tropicopolitan. All of the evidence indicates that it was originally an African species which has spread over the world in post-Colombian times. Ecologically, it is one of the mosquitoes that breed in container habitats: the whole series of special places that accumulate small reservoirs of water under tropical forest conditions, from rot holes in trees and erosion holes in rocks to bits of water in leaf axils or flowers. The ecology of these container habitats has been much neglected, perhaps because they are relatively trivial in high latitudes, though in the tropics the whole canopy of the rain forest can be looked at in one way as a vast aerial swamp. There are hundreds of species of mosquitoes specialized for life in these container habitats, as well as a host of other kinds of aquatic organisms.

The activities of man have also created a variety of special water containers, from vases and tin cans to wells. *Aedes aegypti* moved into this man-made niche. It bred readily in the water kegs of the old sailing ships, and thus got all over the world. What characteristic of the species allowed it to join the human entourage, while its relatives remained in the forests? In parts of Africa, *aegypti* still lives in forests, remote from human activities. But in the rest of the tropical world it is always closely associated with man. Why hasn't it penetrated forest communities in tropical Africa or Asia? Is it that it cannot "compete" with indigenous species? What are the species-species and species-environment interactions involved in this situation? Many such large questions, with implications far beyond *Aedes aegypti,* come to mind as one goes through this book. They can surely be tackled experimentally. Sir Rickard has pulled together all of the pertinent information needed as background, making it possible to formulate such questions; and with this background, it ought to be possible to start looking for the answers, of great possible importance in ecological and evolutionary theory.

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[1] Christophers, Sir S. Rickard. 1960. *Aedes aegypti* (L.), the yellow fever mosquito; its life history, bionomics and structure. Cambridge University Press, Cambridge & New York. xii + 739 pp., 86 figs., 50 tables. $14.50.

The Comparative Ecology of Marine Physiologists[1]

It is tempting to believe it is possible to discriminate a physiologist from an ecologist by whether he studies organisms in the laboratory or in the field ("all forms of life in relation to environment" or, "organisms for their own sweet sakes"). The distinction is, in many ways, artificial. Today, both autecologists and synecologists clearly recognize that knowledge of the physiological functioning of the component parts of a community or of a single species in the community is prerequisite to a complete understanding of ecological relationships and are themselves undertaking physiological studies. Information on the physiology of the components of many communities is non-existent or not readily available, however. Marine ecologists will be happy to note the publication of the present volume, which collates and organizes much of the recent research on the comparative physiology of marine animals.

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[1] Nicol, J. A. Colin. 1960. The biology of marine animals. Interscience Publishers, Inc., New York & London. 707 pp., illus. $14.00.

The title is grossly inappropriate. Nicol clearly states in his preface that he is considering the comparative physiology of marine organisms, not their general biology. Thus, reproduction, embryology, genetics, taxonomy, detailed anatomy, distribution, and synecology are discussed only in passing. Physiologists of the type that regard a particular animal as the "material of choice" for studying a particular phenomenon frequently do not care if it is marine or not. Other physiologists are decidedly concerned with the fact that marine organisms are living (in the most active sense) in a particular kind of environment. It is for the latter that this book has been written and it is this viewpoint that makes the book of genuine interest and use to ecologists.

The fifteen chapter headings are conventional ones for the most part: water, salts and minerals; respiration; digestion; nervous system and behavior; etc. Pigments and color changes are considered in two chapters, another is devoted to mutualism of various degrees and a final one to skeletal and defensive structures. An introductory chapter briefly discusses the basic physical and chemical features of marine habitats. Succeeding chapters are divided into sections dealing with mechanisms, structures, or phenomena. In each section there is a discussion of general principles followed by a treatment of specific phenomena with either illustrations drawn from a variety of animals, or an extended phylum-by-phylum discussion of the phenomenon. Sensory perception and nervous coordination receive the most extended treatments as a result of the great activity in these fields. Respiration studies also are considered at length, possibly as a result of the comparative ease with which studies of oxygen consumption are made.

Noting chapter headings and general organization immediately invites comparison with Prosser's COMPARATIVE ANIMAL PHYSIOLOGY[2]. Both works cover essentially the same type of material, and in very similar styles. In considering only marine animals, Nicol produces a volume that is logically consistent and with a single frame of reference. The great variety of adaptive mechanisms that have been developed by organisms living in the same general environment of salty water, may be profitably compared.

For the most part, the author has been conservative in the facts he has chosen to present and in their interpretation. Many interesting and unique animals and phenomena are not included, in the apparent striving for balance without bulk, and no doubt favorite examples will be missed by some readers. The final choice must be the author's and the result is indeed a balanced one. Only relatively recent references are cited, a fact which immeasurably aids the exposition but sometimes gives no clue to the historical development of a concept. The references are grouped at the ends of paragraphs or sections, rendering them unobtrusive. However, it is very difficult to connect a particular statement with a particular reference.

Nicol has successfully achieved his purpose of both instructing and "diverting." An immense amount of information is presented with no circumlocution. Unfortunately, a uniformly didactic style, each sentence a short, terse statement of fact, is not conducive to browsing. The book is well illustrated and well indexed. An expanded table of contents in future printings would be very helpful, especially since the text itself is very well organized, with a variety of sub-headings.

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[2] Prosser, C. L. 1950. Comparative Animal Physiology. Philadelphia and London: W. B. Saunders Co., 888 pp., 312 figs., 78 tables.

THE SYSTEMATICS OF FRESH WATER BIOLOGY[1]

The scope of aquatic biology from the point of view of the student of fresh water biotas has increased many-fold during the 40 years between the times of publication of the two editions of Ward and Whipple. (Ward, H. W. and G. C. Whipple. FRESH-WATER BIOLOGY. John Wiley & Sons, Inc., New York. ix + 1111 pp., 1547 figures. 1918). As the editor of the second edition has said, if the second edition were presented in the same format throughout as the first it would be a much larger volume. It is unfortunate that this format was not used, from the point of view of a person interested in studying the entire spectrum of organisms which can be found in fresh waters. From the point of view of the student entering upon a career in aquatic biology it is unfortunate that the volume is as large as it is, that it was not divided into two parts, or that the excessive cost of publication of such an ambitious project was not absorbed through bequest, grant, or some other way. However, for those who can afford it, and for those who must use it on the reference shelves of their library or laboratory, it can be a very important tool, although not the only tool, for indentification of members of aquatic biotas.

In the first edition there were four chapters devoted to a general statement of the problems of aquatic biology, a summary of the organisms involved, their conditions of existence, the general ecology, synecology, and ecosystems of the habitats involved, methodology of collecting specimens, data and photographs, and a description of some of the problems encountered by the fresh water biologist. The editor of the second edition has seen fit to let the reader turn to texts on limnology, ecology, and aquatic biology for much of this material. He is concerned to a greater extent with identification and geographic distribution, so that the book becomes a manual for identification to a greater extent than its predecessor. Even techniques of collection, preservation and study are minimized.

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[1] Edmondson, W. T. (editor) 1959. Fresh-water biology (H. B. Ward & G. C. Whipple), second edition. (symposium) John Wiley & Sons, Inc., New York; Chapman & Hall, Ltd., London. xx + 1248 pp., 2551 figs., taxonomic keys. $34.95.

The addition of 15 chapters including descriptive keys to various groups of organisms indicates something of the extent to which modern taxonomy has been concerned with the organisms involved. In some cases the extra chapters represent a splitting up of single chapters in the earlier edition. Where aquatic insects were treated in one chapter before, they are now considered in 10 chapters including an over-all introductory chapter. This section alone could be most useful as a separate publication for those persons interested in aquatic entomology. Chapters on fungi and bryophytes have been added, while chapters on parasitic flatworms and roundworms, and aquatic vertebrates have been dropped.

In the new edition two general types of keys are used. The first may be referred to as that in which the style of the old format is used. Here relatively brief, or longer descriptive, key characters are used, interspersed with descriptive and distributional material, and including at appropriate points illustrations of the organisms involved or of those parts of the organism used in critical identification. The new format for keys is in the form of relatively simple key characters without additional information. In some cases additional information of distributional, morphological or taxonomic nature is inserted as a brief note.

It is probably safe to assume that no single reader will be able to use the entire book without assistance from one or more specialists. At the present level of our knowledge of aquatic biota, no one individual can hope to be trained in such a diverse array of organisms as fungi, diatoms, ciliates, rotifers, copepods, insects, mollusks, and bryophytes to the extent that he can understandably use each of the keys in a rapid examination of a sample of material obtained from a stream bed, lake shore, or waste stabilization pond.

R. Y. Stanier's "Introduction to the Protista" is an outstanding contribution to the understanding of the place of the lower organisms in the scheme of life. It may not go as far in all the directions that Whittaker or Copeland would like but it goes far beyond the traditional concepts of the groups involved, and presents a workable pattern for the distribution of such organisms within morphological and ecological working groups.

Within certain groups of organisms the illustrations which are used are all new. This applies to those organisms falling within categories previously untreated, or categories in which the new monographer finds different illustrations best suit the purpose. In some groups all illustrations are taken from the plates used in the first edition. In other groups some of the illustrations were borrowed from the older text, others are new. Usually the newer illustrations are more clear, more adequate, and do not show the wear of years of storage.

The groups of organisms treated and the monographer responsible for the treatment are as follows: *Bacteria* C. B. van Niel and R. Y. Stanier; *Fungi* F. K. Sparrow with *Fungi Imperfecti* by W. W. Scott; *Myxophyceae* Francis Drouet; *Algae* (except Blue Green Algae and Diatoms but including flagellate groups) R. H. Thompson; *Bacillariophyceae* Ruth Patrick; *Zooflagellates* J. B. Lackey; *Rhizopoda* and *Actinopoda* G. Deflandre; *Ciliophora* L. E. Noland; *Porifera* Minna E. Jewell; *Coelenterata* Libby H. Hyman; *Turbellaria* Libbie H. Hyman and E. Ruffin Jones; *Nemertea* W. R. Coe; *Nemata* B. G. Chitwood and M. W. Allen; *Gordiida* B. G. Chitwood; *Gastrotricha* R. B. Brunson; *Rotifera* W. T. Edmundson; *Bryozoa* Mary Dora Rogick; *Tarigrada* E. Marcus; *Oligochaeta* C. J. Goodnight; *Polychaeta* Olga Hartman; *Hirudinea* J. P. Moore; *Anostraca* R. W. Dexter; *Notostraca* F. Linder; *Conchostraca* N. T. Mattox; *Cladocera* J. L. Brooks; *Ostracoda* W. L. Tressler; *Free-Living Copepoda* Mildred S. Wilson and H. C. Yeatman; *Branchiura* and *Parasitic Copepoda* Mildred S. Wilson; *Malacostraca* F. A. Chace, Jr., J. G. Mackin, L. Hubricht, A. H. Banner, and H. H. Hobbs; *Introduction to Aquatic Insecta* H. H. Ross; *Ephemeroptera* G. F. Edmunds, Jr.; *Odonata* Leonora K. Gloyd and Mike Wright (posthumously); *Plecoptera* W. E. Ricker; *Hemiptera* H. B. Hungerford; *Neuroptera* A. B. Gurney and Sophy Parfin; *Coleoptera* H. B. Leech and M. W. Sanderson; *Trichoptera* H. H. Ross; *Lepidoptera* P. S. Welch; *Diptera* M. T. James; *Acari* I. M. Newell; *Mollusca* W. J. Clench; *Bryophyta* H. S. Conard; and *Vascular Plants* W. C. Muenscher.

It might be suggested that should another edition of this volume be produced at some future date, consideration be given to allowing space for the inclusion of aquatic lichens, soil fungi which have returned to an adventitious life in stream and lake waters, the parasitic groups which were dropped from the present edition, and the aquatic vertebrates. Depending on the amount of information the writers of the several mongraphs, upon which such a project would be based, would desire incorporated, the work could be arranged in more than one volume, the whole of which would be available in libraries and laboratories requiring such information, the parts available to students of specialized groups such as the Protista, the Insecta, the Fungi, animals exclusive of insects, and plants.

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CINCINNATI

PLANTS AND ENVIRONMENT[1]

The essence of the first edition of Professor Daubenmire's textbook remains little changed in its second edition, although substantial parts of the text have been rewritten and expanded to incorporate new knowledge. The contents and sequence of presentation are summarized in a review of the first edition by H. P. Hansen in ECOLOGY **29**: 398-9.

The orderly arrangement of information gives the book much of the character of a reference manual, but the style is more expansive and the general impression gained from reading the book as a whole is that it presents a clearly written and comprehensive analysis of the physical factors which constitute plant environment. Clarity of discussion demands some isolation of factors, but the ecological viewpoint is emphasized by Professor Daubenmire's adequate cross-referencing and insistent reminders to the reader that factors interact in various and often complex ways. This is one solution to an outstanding difficulty in teaching ecology; the need to instill a true appreciation of the intricate complexity and constant flux of habitat conditions without simultaneously producing a feeling of bewilderment or despair in the student.

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[1] Daubenmire, R. F. 1959. Plants and environment: A text-book of plant autecology. 2nd edition. John Wiley & Sons, Inc., New York; Chapman & Hall, Ltd., London. 422 pp., 14 tables & 92 figs. $6.95.

It is precisely because of this need to regard the environmental complex as a whole, however, that Professor Daubenmire's treatment seems unrealistic, in that the individual organism is lifted almost entirely from the vegetation of which it is a part, when the impact of general physical environmental factors are discussed. For example, out of fifty-three pages devoted to analysis of temperature factors, the influence of plant cover on temperature is disposed of in one page, yet in most communities the individual organism experiences a highly modified microclimate because of the profound influence of its neighbours. Of equal importance is the neglect by this approach of the concept of competition (a word which incidentally does not even appear in the index). While it is true that competition must to a large extent operate through modification of the physical system by some species in a way advantageous or deleterious to others, it is surely important to emphasize its manner of operation and effect.

Competition can only be neglected when exploring the broadest physiological limitations of a species, and its importance must be considered when using experimental results to interpret behaviour in natural environments. This is because a major obstacle in the experimental-autecological approach to ecology lies in the fact that plants often grow well in conditions from which they are nevertheless naturally excluded by even better-adapted species, and plants will often thrive under artificial combinations of conditions which are never realized in nature. This must not imply that a physiological and experimental approach to ecology is not the best, but there is a very real risk that the student gains a false impression of the simplicity of the direct approach. Even at this level a textbook should illustrate how such work requires a flair for the design of experiments which simulate field conditions and yet allow adequate control and sufficient uniformity to permit replication. Usually the application of experimental information to field problems is facilitated by attacks at several levels of refinement and control; these may range from experiments in the field, to studies in the experimental garden, greenhouse and controlled-environment growth-chamber.

Perhaps this general criticism really hinges on Professor Daubenmire's concept of autecology, for so much of the material included in his book is discussed in very general terms and concerns plant life as a whole, rather than demonstrating why certain habitats differ in ways more favourable to some species than others. It seems surprising in a textbook of plant autecology that much more attention is not given to the elucidation of different ways in which different species respond to the same environmental conditions, as is done, for instance, in the discussion of compensation points of tree seedlings. In contrast, there is almost no discussion of soil preferences of different species, nor the possible underlying physiological differences which may cause them.

The analysis of the way in which species differ in their responses under similar circumstances is surely the outstanding feature of autecology. These comparisons are best illustrated by setting out carefully chosen experimental and analytical information, but Professor Daubenmire imposes a severe limitation on himself by intentionally avoiding giving original data and specific examples. This omission gives the text a rather abstract form and many fascinating subjects are mentioned and not pursued. A feature of very great value to the student, on the other hand, is the book's synthesis of information from several other branches of science. Relevent aspects of physics, chemistry, meteorology and so on are discussed, so that no one can escape the conclusion that an ecologist requires a broad scientific background. A chapter on fire as a factor in plant ecology has much of interest and includes two tables of primary data to illustrate the important changes in the soil following forest fire.

In a book which ranges over such a wide field of knowledge it is easy to find small points here and there which are open to criticism, but in broad outline the treatment is excellent. A more general criticism can be made of the section devoted to soil chemistry, where many important features are treated in a peculiarly imprecise manner which leads in some instances to incorrect or obscure statements. In the section on the water relations of soils and plants several pages are devoted to the discussion of the permanent wilting point and several statements suggest that plants automatically die at this level of water stress (p. 119), whereas there is evidence, which is mentioned subsequently, that many plants survive in much drier soils and will even continue to withdraw water. Important differences in the survival of plants after wilting need to be stressed. Too much attention to the permanent wilting point distracts attention from the very severe reduction in growth rate which may arise from water shortage at very much lower water tensions; this may operate either at a critical stage in establishment and thus reduce leaf area or over long periods during the development of the plant.

The book has the high quality of production of so many American textbooks, it is strongly bound, beautifully printed on high-quality paper and illustrated with a carefully selected set of photographs. Possibly not enough use is made of line drawings and graphical presentation, and several discussions could be clarified and made more concise by relying on this method.

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Tropical Forests and Vegetation Analysis[1]

Professor Cain has had the good fortune both to visit and to work in what is probably the largest area of primary tropical rain forest in the world. With his previous wide experience, he is well equipped to investigate the suitability of quantitative and phytosociological methods for the analysis of tropical vegetation. The co-author of this book, Dr. Castro, has been studying vegetation for the Brazilian Serviço Nacional de Malaria.

After it has been pointed out that plant geography includes the distribution of both species and vegetation there are short, but sound, chapters on "Floristics" and "The Community." Then follows a chapter entitled "Major Vegetation Types of the World, with the Tropical Rain Forest as an Example." Types of world vegetation and types of tropical vegetation, according to Beard's classification, are briefly discussed, followed by sixty pages on the tropical rain forest itself in order "to focus attention primarily on rain forest as an example of vegetation analysis applied to a world formation." The procedure adopted in this chapter is different from that in the rest of this book in that is is mainly descriptive ecology. The associations within the forest, its very great floristic richness, the various synusiae, the general morphology of the trees, and other features of the tropical rain forest, with special reference to South America, are described.

The remaining 180 pages of this book are devoted to vegetation analysis for "the *Manual* is concerned largely with methodology." The subjects dealt with in the five earlier chapters of this part include: sampling methods, abundance and density, frequency, species-area relations, minimal area, dominance, coverage, sample size, etc. Most of these subjects are well covered in a non-mathematical manner which will no doubt please many biologists. The chapter on "The Combination of Community Characteristics" gives a good critical account of the Braun-Blanquet system followed by a summary of the methods used by Curtis and his colleagues and ends by mentioning the system of Dansereau. The concepts of presence, constancy and fidelity are well dealt with in the next chapter. Finally there is a chapter entitled "Life Form and Leaf Size" in which the various life forms are described. Following an account of the simple life-form spectrum, in which all species are treated as equals, various ways in which individual species may be weighted according to some measure of their quantity, are discussed. Leaf sizes are treated similarly. The examples chosen to illustrate items in this, the major part of the book, are from all types of vegetation but a good many are from South American forests.

Finally there are a useful Glossary, the Literature Cited and an Index.

What is the purpose of this book, or *Manual* as it is called, and to whom is it addressed? The Preface hardly helps here: "it occurred to us that our experiences would have more value for the Serviço Nacional de Malaria if we prepared a small manual of concepts and methods . . . the manuscript continued to grow beyond the original intent . . . the *Manual* is in no sense a study of Brazilian vegetation, but it does recognize the existence of the tropics and some its problems, and that is something."

The book, as a whole, has no coherence: there are three disunited parts although the authors do not recognize these as such; the introductory chapters, a description of tropical rain forest and, occupying only just over half the book, what might be termed 'the manual itself.'

It would rather appear to defeat the purpose of the *Manual* to commence the section on the tropical rain forest with the paragraph:

> "Just as a literary description may convey more meaning of some particular manifestation of weather and climate which one has not personally experienced than would a book full of instrumental data, so a vivid description of tropical rain forest may have its place in introducing us to more precise considerations. This purpose can be served by a rather lengthy quotation from *The Naturalist in Nicaragua* by Thomas Belt."

and end it with the remark "that rain forest (in a generic sense) cannot be treated quantitatively." Much of this chapter describing the tropical rain forest is sound but, to one familiar with this vegetation type, often naive.

In 'the manual itself' many of the subjects are treated historically; a manner which is of doubtful value and much space is taken by repeating old controversies, especially phytosociological ones. The subjectivity or objectivity of phytosociological methods is discussed at length with only a passing reference (in the introduction) to the important series of papers by Poore. Indeed, one has the impression from the literature cited that recent work on many of the topics discussed has been largely ignored. One good point is the inclusion of a concise account of Raunkiaer's system of plant life forms, which is of considerable ecological value and is all too often a neglected factor in the description of vegetation. One major criticism is that the various methods are discussed without any reference as to their ecological value, the purpose in recording them, or how to deal with the data collected.

There are many minor cirticisms such as the danger in quoting introduced species as examples of curious phenological behaviour, also confusion might be caused by placing different numbers of samples in figures 14 and 15. The book is generally well produced but appears to have been rather hurried for there are numerous printing errors some of which, such as the use of M. E. for M_E on page 149 and the misquotation of Evans' "oak-hickory" as "oak-history" in figure 26, might be misleading. Also, in the copy received, the printing was not uniformly black.

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[1] Cain Stanley A. and G. M. de Oliveira Castro 1959. Manual of vegetation analysis. Harper & Brothers, New York. xvii + 325 pp., 45 figs., 74 tables. $7.50.

Vegetation Analysis for Students[1]

Practical handbooks for teaching purposes are very popular in the United States whereas most British biologists, including the present reviewer, regard them with little enthusiasm. It is therefore a pleasant surprise to find one of these books which is almost above criticism.

The title is misleading; it ought to have been called "Methods of Vegetation Analysis," for vegetation study implies the correlation of vegetation with its environment, a subject not mentioned.

This book is 8¼″ by 5½″ and slim so that it would fit into a large pocket, or at least into a rucksack or haversack. Its cover might be waterproof, but this is not stated and an experiment was not thought desirable. It contains 25 chapters arranged in seven parts and includes a total of 56 exercises. The subjects dealt with include: mapping, physiognomic methods and life forms, frequency, abundance and density, cover and basal area, transects, point quadrats, succession, presence and constancy, the continuum, vegetation formulae, and various more advanced techniques. Finally there are lists of literature cited, books for class use, ecological and other journals, and instruments and equipment required.

A student who has worked through even a majority of these exercises will have had a very good ecological training. As in most of these books some parts are grossly over-simplified (e.g. the procedure for the 'stick and radius rod method' of setting up circular quadrats) and others are quite advanced and assume considerable theoretical knowledge (e.g. the use of contiguous quadrats to determine the type of distribution of plant individuals). The student is, quite correctly, constantly told to observe a large number of samples; preferably at least one hundred often being stated. Also, almost all the exercises end with good questions; this should be the basis of university teaching—to make the student think for himself.

There are several minor blemishes: there are easier ways of obtaining random numbers than the method given in Exercise 11; there is no mention of trenching or peat boring in the chapter on "Succession in Place"; there are several loose generalizations such as the statement that "many ecologists in Great Britain prefer to estimate abundance by the use of scales"; and the title of Exercise 5 ("Profile diagrams of many British ecologists") might be misleading!

The book is well produced, and printing errors are rare. Altogether this is a delightful little book.

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[1] Phillips, Edwin Allen 1959. Methods of vegetation study. Henry Holt & Co., Inc., New York. xvi + 107 pp., 17 figs., 10 tables. $2.95.

Ecology and Agriculture in Africa[1]

Dr. Phillips is particularly well qualified to write this book. He has carried on research, teaching, and surveys in many parts of Africa since 1922 as an ecologist, forester, and agriculturist. His long association with General Jan C. Smuts, the "wisest ecologist" Phillips ever knew (and he has known many), was most inspirational and practical. Dr. Phillips, although realizing that so much needs to be learned about Africa, was impelled to write this book for the following reasons.

1. To attempt to assess the future development of agriculture in Africa.
2. To hasten the awakening of Africans and others to the necessity of adjusting traditional practices to the rapid social, economic, and environmental changes.
3. To emphasize the necessity for European and African of altering their attitude to arable and pastoral farming.
4. To stress the need of studying the ecological bases for agricultural and related development before attempting further large-scale mechanized or other ventures.
5. To call attention to facets in the ecological and economic readjustments in the principles and practices of land tenure, particularly as related to shifting cultivation.
6. To aid in laying the foundation for ecological planning in the accelerated tempo of agricultural, economic, social, and political development.

The ecological basis of the book includes classification of Africa South of the Sahara into 10 major divisions as follows: 1. Highly humid forest, 2. Subhumid wooded savanna and related vegetation, 3. Mild subarid wooded savanna, 4. Subarid wooded savanna, 5. Arid wooded savanna and related vegetation, 6. Subdesert, 7. Desert, 8. Open grassland, 9. Macchia or maquis, and 10. Edaphic communities, especially mangroves, swampland, and dunes. The first 9 of these divisions, called climax or bioclimatic regions, are differentiated bioclimatically. The excellent, original vegetation map in color depicts these major regions with many subdivisions.

This volume has 5 main parts or "books." The first part deals with the scope, background of the problems, soil hazards, and problems set by wild and domesticated animals. The second and third parts describe the ecological and vegetation conditions and the potentialities of agricultural and related development of the various major regions. The fourth part is concerned with problems of human and animal health and of economics and planning in agricultural and related development. The fifth part gives general conclusions and suggestions, discussing failures and advice for the way ahead.

The bibliography contains more than 650 references and the index is satisfactory. The author merits appreciation for his extensive study and hard work in preparing this exhaustive book and the publishers have done an excellent job in typography and binding.

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[1] Phillips, John. 1960. Agriculture and ecology in Africa. A study of actual and potential development south of the Sahara. Faber & Faber, London; Frederick A. Praeger, New York. 424 pp., 26 tables, map 63, $13.50.

CONSERVATION AND WATER MANAGEMENT[1]

It is likely that every member of the Ecological Society will be interested in a series of four remarkable pamphlets recently published by Luna B. Leopold under the title CONSERVATION AND WATER MANAGEMENT. The titles of the four papers, all originally given as public addresses, are "Conservation and Protection," "The Challenge of Water Management," "The Conservation Attitude," and "Ecological Systems and the Water Resource." These titles speak for themselves, to a certain extent, in indicating the main themes of the papers. However, they do not even suggest the depth or clarity of the author's penetration into the philosophy of conservation and the heart of the subject of human ecology. The author is the Chief of the Water Resources Division of the U. S. Geological Survey, and not the least of the interest of the papers is their indication that there is at least one high government official in a field intimately connected with conservation who realizes, and is not afraid to say, that there are things of importance to man which cannot be assigned a money value and that we should conserve these things in spite of this lack of an economic motive. Especially would we recommend Leopold's analysis and presentation of the conservation attitude, in the third of these papers.

F. R. FOSBERG

FALLS CHURCH, VA.

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[1] Leopold, Luna B. 1960. Conservation and Water Management. Geological Survey Circular 414 A-D, Washington, D. C. 26 pp. Available gratis on request to U. S. Geological Survey, Washington 25, D. C.

HUMAN ECOLOGY, AND CONNECTICUT'S TWO ROADSIDE BULLETINS[1,2]

I am in complete agreement with the synopsis of the points stressed in this bulletin. I think the roadside spraying program is way out of line and hope that the men responsible for carrying out the program will follow the principles outline in this bulletin."—from a letter to one of the Arboretum authors, from the Director of Research in agricultural chemicals of a leading chemical manufacturer.

Because these two bulletins have a significance far beyond the irrational and out-of-hand Connecticut situation that gave birth to them, because the lessons they teach are important both on the national and international scenes, this review appears warranted. The review is intended to transcend a mere cataloguing of contents, to consider both bulletins for what they are and what they are not, and therefore how they fulfill the role for which the authors intended them and of which Society has a need. These latter functions lie in the realm of "human ecology." My qualifications as reviewer may be thought either exceptional, or qualified by close involvement, for I may admit a palpable paternity in regard to some of the ideas emanating from the Connecticut Arboretum on this subject. On the other hand, the biology involved is of the very simplest kind, so simple that it cannot possibly start a valid scientific controversy. Last summer at Montreal I deplored the relative absence of scientific literature in this field, to which moan F. R. Fosberg replied with mock scorn that "what good botanist would bother to waste his time on the perfectly obvious!". Some botanists are bothering. They are a varied group, ones who have a cynical interest in human ecology, who have an altruistic interest in conservation, who are preened by the blandishments of industry, or who—like one of the authors here reviewed—may be innocently caught in a social web not of their own making.

More seminatural roadside vegetation is seen by more people more often in the U.S.A. than any other type of land. The very extent of that land is astonishing: in the aggregate, the entire area, including pavements, was estimated by Charles Morrow Wilson in 1955 to be equal to that of Georgia, largest state east of the Mississippi. The management of this land has not had the benefit of those botanists most fit to contribute to it, the ecologists managing plant-communities. To the contrary it has served as a free-for-all for several commercial and political groups, the producers, sprayers, and consumers of herbicides. Too frequently, a public-be-damned attitude has developed. If the public has the cheek to protest, it feels the full force of persuasive and manipulative techniques. Such techniques are amazingly effective on an otherwise uninformed and guillible public. One device tried this spring in Connecticut, and at least temporarily effective, is for industry to "educate" a leading non-profit conservation organization, and then speak through its mouth. American roadsides need help. The professional organization best suited to aid is the Ecological Society of America, but so far it has proven itself unaware, uninterested, or inept.

The Connecticut Arboretum bulletin by Goodwin and Niering, with a major 7-page article entitled "The management of roadside vegetation by selective herbicide techniques," packs a large amount of common sense and sound botany into a small space. The authors offer recommendations, within the physical needs of the highway engineer and of the utility engineer managing adjacent phone and power lines, and with due recognition of immediate and ultimate costs. The kinds of chemicals, the techniques of spray treatment, the problems of ragweed and poison ivy are all discussed. The figure on page 7 tells the phytosociologic story in recommending the *selective* application to tree sprouts so as to *root*kill them, leaving the food-and-cover-desirable and landscape-desirable shrubs to form a tight community that resists the *re*invasion of tree seedlings. I myself would certainly have added another figure, showing a 20-times blanket-sprayed roadside, much of the original ash and maple still alive, the shrubs long gone, an abundance of annual grassy weeds, and enough bare land to fill up with ragweed whenever spraying is stopped. Such a figure however would have been "controversial." The Arboretum bulletin is not designed as a how-to-do-it manual. On the other hand, I have never yet, in 14 years, found a major contractor who did not say he could do this kind of selective work—"if the client asks for it."

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[1] Goodwin, Richard H., and William A. Niering. 1959 (March). A roadside crisis: the use and abuse of herbicides. Connecticut Arboretum (New London) Bull. 11, 13 pp., illus. *Republ. in* Plants & Gardens (Brooklyn 25), annual digest issue, **15**(4): 4-7. 1960 (February).

Ahrens, John F. 1959 (May). Chemical control of weeds and brush along roadsides. Connecticut Agricultural Experiment Station Bull. 624. 32 pp., 4 figs.

[2] The additional length of this review has been made possible by a grant from the Connecticut Botanical Society. I express my appreciation to Drs. Goodwin and Niering for corrections to the original manuscript of this review. Dr Ahrens writes that "I feel it would be unethical for me to comment on it [the manuscript] before publication. For this reason I prefer not to see it at all."

The Connecticut Agricultural Experiment Station bulletin is representative of a social situation, by no means unique, whereby a group of sound, competent, and respected scientists can, through unwise but understandable administrative decisions, hand assignments to wrong parties for supposedly routine projects, and turn out publications which in the hands of certain groups worsen the very situation they aimed to benefit. This statement is in no manner whatever to be construed as a professional indictment of the Station or its personnel. It is a cold human-ecologic comment upon the American scientific scene, in which the high degree of specialization may leave specialists and administrators unaware of their unawareness not only of the common tenets of certain specialities but even of the specialities themselves. In this instance, the writing of the bulletin was assigned to Dr. Ahrens. A respected plant ecologist who might have much to say on the matter was bypassed, and has remained silent. Without judgment on this case in particular, a problem of growing significance to the scientific community, and interesting questions as to the freedom of a scientist in matters of social significance, either imposed from above or self-imposed for reasons of job security, are suggested.

The assignment to Dr. Ahrens, I assume, was because he had been involved with "weed control" on agricultural lands. There is certainly a relationship, in that both agricultural weed control and and roadside vegetation management utilize herbicides. There the similarity stops, for in the former case we are dealing with the lives and deaths of individual plants, in a perspective mainly of one year. In the latter, we are dealing with the lives and deaths of plant communities, planning for 25 years, with an entirely different intellectual and technologic approach. To my knowledge, Dr. Ahrens is a wholly competent plant physiologist and agronomist, and his bulletin reflects a thorough if plodding survey and abstracting of the herbicide literature within his grasp. I myself find it a handy reference to such matters as a survey of the chemical herbicides used, problems of volatility, drift, weather, poisonous qualities for animals, calibration of spray equipment, the various kinds of woody plant treatment, and special treatments for critical species (but not for ragweed, that gives industry one of its biggest excuses for pushing unwise spraying techniques). A 2-page list of foliage-spraying susceptibilities to 2,4-D and 2,4,5-T ignores the far more effective basal and stub-spraying techniques for woody plants, in the literature for over a decade. It is the bibliography which opens one's eyes. Of 65 references, 37 are directly from the PROCEEDINGS of the Northeastern Weed Control Conference (The Conference, meeting once a year, is "sustained" by about 35 commercial organizations, and could be the subject of a most interesting objective study by any social psychologist); 5 references are from the journal WEEDS (the journal of the Weed Society of America, previously called the Association of Regional Weed Control Conferences), seven are from corporation bulletins. In Dr. Ahren's bulletin, there is no adequate recognition of the belts of roadside vegetation: scraped shoulders, mowed strips, shrubby sides, each with its own vegetation problems. There is no recognition of the important differences between leafkill, shootkill, and rootkill, and of the baring of the soil for subsequent invasion by other weeds. The all-important subject of the sociologic stability of the post-spraying vegetation, involving the trees which can and do reinvade certain communities, is missing. The significant forestry literature on hazel thickets and on rhododendron slicks is ignored. The entire science of phytosociology is conspicuous by its absence, and the art of Vegetation Management is nowhere apparent.

The impact of these two roadside bulletins on the local social scene is extremely instructive. It has developed a situation that might amuse a misanthropic anthropologist, even while it furrows the eyebrows of the social-minded conservationist. A real value however lies in its instructive features, for those operating in the fields of applied ecology and conservation. The Arboretum bulletin, representing sound scientific knowledge that is commercially practicable, is considered "controversial" in that, though it has the support of every conservation group in the state that has considered the issue, the government groups have maintained an aloof silence. The Experiment Station bulletin follows conventional station policy in not taking sides (regardless of how scientifically absurd a controversy may be), not promoting, not criticizing, but merely offering information which can be asked for (an approach which may leave one at a woeful disadvantage if other social forces do not have the same kind of ethics). This bulletin was originally planned as a source of authoritative information for the Selectmen and Town Clerks of Connecticut's 169 Towns, whose education in this subject was predominantly that imbibed at cocktail parties and other meetings run by industry. The result could have been predicted. The Station bulletin has been grasped by industry, as an encircled platoon welcomes an airlift of ammunition. Dr. Ahrens has become the new "brush control authority," welcomed at commercial or pseudo-commercial meetings, to whom all questions are referred. The bulletin is quoted as the unquestionable authority, supporting the spraying programs of our leading electric utility and our phone company. (But how Fanny Farmer's cookbook, as a collection of recipes, could be held up as an authority in community dietetics, would be an amusing but serious distortion of our Fanny's first function). I do not know the answer to this impasse in conservation. It does not involve merely pin money. (One state, with an extra thousand miles blanket-spray this year, is slowly but surely succumbing to a 20-million-dollar 5-year contract to cover its entire mileage—and this is only a start). The problem is an integral part of the American scene, involving not only a biologist's unawareness of significant developments in fields not his own, but an equal unawareness of the larger social scene in which he may easily become a mere puppet, all mingled with notions of security and of freedom that are not necessarily compatible. In this instance, the wise use of an acreage equal to the state of Georgia is at stake. It is not that we need more biologic knowledge: enough exists to warrant controlling legislation. Perhaps biologists by nature simply do not have the social consciousness and skill, or the courage, to apply that knowledge. The passage of time is giving the answer.

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CORRECTION

In the article "Single-factor analysis in population dynamics" by R. F. Morris, Ecology 40, No. 4, October, 1959, p. 581, column 1, third line from bottom, for "0.0602" read "0.602."

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